



Zootaxa 4499 (1): 001–087

<http://www.mapress.com/j/zt/>

Copyright © 2018 Magnolia Press

Monograph

ISSN 1175-5326 (print edition)

ZOOTAXA

ISSN 1175-5334 (online edition)

<https://doi.org/10.11646/zootaxa.4499.1.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:A191D47C-AA66-4A95-8ED1-2B494EFC8F0E>

ZOOTAXA

4499

Alternative facts: a reconsideration of putatively natural interspecific hybrid specimens in the genus *Heliconius* (Lepidoptera: Nymphalidae)

ANDREW V. Z. BROWER

Evolution and Ecology Group, Department of Biology, Middle Tennessee State University, Murfreesboro, TN 37132 USA.

E-mail: andrew.brower@mtsu.edu



Magnolia Press
Auckland, New Zealand

Accepted by C. Prieto: 26 Apr. 2018; published: 12 Oct. 2018

Licensed under a Creative Commons Attribution License <http://creativecommons.org/licenses/by/3.0>

ANDREW V. Z. BROWER

Alternative facts: a reconsideration of putatively natural interspecific hybrid specimens in the genus *Heliconius* (Lepidoptera: Nymphalidae)
(*Zootaxa* 4499)

87 pp.; 30 cm.

12 Oct. 2018

ISBN 978-1-77670-500-9 (paperback)

ISBN 978-1-77670-501-6 (Online edition)

FIRST PUBLISHED IN 2018 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: magnolia@mapress.com

<http://www.mapress.com/j/zt>

© 2018 Magnolia Press

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of contents

Abstract	3
Introduction	3
Methodology: a scorecard of reliability	4
Notes and reliability scores for individual <i>Heliconius</i> specimens in the Mallet et al. (2007) database	7
Putative hybrids of various silvaniform <i>Heliconius</i> species	7
Putative hybrids between <i>H. ethilla narcaea</i> and <i>H. besckei</i>	23
Putative hybrids between various races of <i>H. cydno</i> and <i>H. melpomene</i>	25
Putative Central American <i>H. melpomene</i> x <i>H. cydno</i> hybrids	25
Putative hybrids between <i>H. melpomene cythera</i> and <i>H. cydno alithea</i>	29
Putative <i>H. cydno cydno</i> x <i>H. melpomene martinae</i> hybrids	34
Other Colombian putative <i>H. cydno</i> x <i>H. melpomene</i> hybrids from the Magdalena Valley	45
Putative <i>H. cydno cordula</i> x <i>H. melpomene melpomene</i> hybrids from Venezuela	56
Putative hybrid between <i>H. heurippa</i> and <i>H. melpomene melpomene</i>	64
Putative hybrids between <i>H. cydno galanthus</i> and <i>H. pachinus</i> from Costa Rica	67
Hybrids between <i>H. erato</i> and <i>H. himera</i> from western Ecuador and Peru	68
Putative <i>H. erato</i> x <i>H. charithonia</i> hybrid	73
Putative <i>H. charithonia</i> x <i>H. peruvianus</i> hybrid	74
Putative <i>H. hecalesia</i> hybrids	75
Discussion	78
Conclusion	82
Acknowledgments	83
References	83

Abstract

Mallet *et al.* (2007 *BMC Evolutionary Biology*, 7, 28) employed a database of putative interspecific hybrid specimens of the genus *Heliconius* to advance a hypothesis of "the species boundary as a continuum." Here, each of those specimens, as well as subsequently documented specimens, is individually reassessed regarding its phenotype, potential parentage and chain of custody in collections. Using a quantified scale of reliability, most of the specimens are interpreted differently than Mallet *et al.*'s identifications, and the actual number of interspecific hybrids is estimated to be much smaller than they proposed. To be specific, of 163 putative hybrid specimens examined, 11% suffered from ambiguous identity, 5% from confounding issues with their data labels, 50% were arguably intraspecific (depending upon alternative species concepts), and 22% were almost certainly reared, commercial specimens. Only eleven of the specimens meet the criteria established here to be legitimate and reliable interspecific hybrids, and all of those are between closely-related species. This result has potentially important implications for current hypotheses of frequent genomic introgression of wing pattern alleles among *Heliconius* clades.

Key words: hybridization, introgression, gene flow, species boundary, hybrid speciation

Introduction

"(W)e would not be able to distinguish species if hybridization were common."—James Mallet (2005)

Heliconius butterflies have long been renowned for their aposematic wing patterns, their interspecific mimetic convergence, and their intraspecific differentiation into diverse geographical races/subspecies (Bates, 1862; Poulton, 1890; Punnett 1915; Eltringham, 1916). According to the latest nomenclatural checklist (Lamas and Jiggins, 2017), the genus contains 48 species and 345 valid subspecies (including nominate and as-yet unnamed forms), in addition to over 1500 published names for infrasubspecific morphs, aberrations and hybrids that are not recognized as available under the ICZN Code (1999).

After extensive study of this bewildering diversity of wing pattern variation in public and private butterfly collections around the world, Mallet *et al.* (2007) published an article characterizing "the species boundary in *Heliconius* as a continuum," invoking as evidence a compendium of atypical specimens that they interpreted as interspecific hybrids. Their dataset had been gestating for nearly a decade prior (Mallet *et al.* 1998), but the 2007 paper was the first to present the raw data, in the form of an online supplemental gallery of images, summarized

label information, and brief conjectures about the putative ancestry of each specimen. The paper has since become widely cited as an empirical cornerstone that establishes the theoretical plausibility of hybrid speciation among *Heliconius* (Mallet, 2008; Salazar *et al.*, 2008; Nadeau *et al.*, 2012; Jiggins, 2017): if evidence that interspecific hybridization occurs can be documented via specimens in natural history collections, then such hybridization can be invoked as an explanation for patterns of wing pattern convergence and other instances of homoplasy, by means of genetic introgression. The Mallet *et al.* (2007) paper thus advanced the phenomenon of interspecific hybridization as part of the "background knowledge" for explaining hypotheses of genomic mosaicism.

The object of this review is to revisit Mallet *et al.*'s (2007) identifications from an alternative perspective and in light of recent discoveries of heretofore unknown *Heliconius* diversity, particularly in the *H. cydno*-*H. melpomene* clade (Giraldo *et al.* 2008; Mérot *et al.* 2013; Arias *et al.* 2017). This paper presents reinterpretations of individual specimens hypothesized by Mallet *et al.* (2007) to be interspecific hybrids. I do not attempt to comprehensively reinvestigate the specimens themselves, but only to assess the evidence, including label information and interpretations of specimen identity, as presented by Mallet *et al.* (2007). The Mallet *et al.* (2007) images were published as open access supplemental material and so may be reproduced here with appropriate attribution. Unless otherwise noted, images of putative hybrid specimens in this article were sourced from https://www.biomedcentral.com/content/supplementary/1471-2148-7-28_12862_2006_322_MOESM1_ESM.zip. All images in this paper are Creative Commons licensed, otherwise freely available on the web, or reproduced with permission from their owners. Numbers on the images below refer to the numeration in the Mallet *et al.* (2007) supplemental material, which may be consulted for original image credits. To facilitate the reader's ease of comparison of images and descriptions, the figures are embedded in the text at the point of first reference, rather than assembled into plates at the end of the text.

Reconsidering this source of raw evidence for interspecific hybridization suggests that the phenomenon occurs much less frequently than Mallet *et al.* (2007) proposed, and that the foundation this dataset has provided for narratives of rampant adaptive gene flow and hybrid speciation cannot be taken as a straightforward assumption.

Methodology: a scorecard of reliability

Inferring the parentage of a pinned butterfly specimen is a matter of "expert opinion," which is to say a subjective judgment, even if that judgment is well-informed by long experience in the field and museum. The evidence is generally derived from the wing pattern—the distribution of different colored scales on the dorsal and ventral surfaces of the fore- and hindwings. Despite their intraspecific variability and remarkable mimetic resemblances, most *Heliconius* specimens can be reliably identified as a particular species or subspecies on the basis of easily-recognized diagnostic features. However, some specimens do not fit these norms and are more challenging. Such a specimen could be a hybrid, a genetic mutant, a phenocopy altered during development, or have a peculiar phenotype due to environmental effects after emerging from the chrysalis, or even potentially after being collected. In order to hypothesize that a specimen is an interspecific hybrid, one should first reject alternative, more parsimonious explanations (of course, what constitutes a "parsimonious explanation" may itself be the subject of debate among experts). Furthermore, given the bewildering geographical variability of many *Heliconius* species, specimens with poor locality data represent additional challenges to interpretation. Here are five questions that address different components of a specimen's credibility and evidentiary value as a putative interspecific hybrid:

Is the hybrid interspecific?

The gold standard for specific distinctness under the biological species concept (Mayr, 1942) is coexistence of two species in sympatry without interbreeding. However, many species of *Heliconius* butterflies (e. g., *H. erato* and *H. melpomene*) exhibit tremendous intraspecific geographical variability, with markedly different-looking geographical races replacing one another across the species' ranges. Most hybrid *Heliconius* butterflies, both living in nature and in collections, are intraspecific, arising from crosses between members of adjacent geographical races of the same species that exhibit different wing patterns. There are many famous intraspecific hybrid zones where such specimens have been encountered for more than a century: in the vicinity of Tarapoto, Peru, in the Cordillera Occidental west of Cali, Colombia, and in the vicinity of St. Laurent du Maroni, French Guiana, to name a few. In several instances, allopatric or parapatric subspecies or geographical races of *Heliconius* have been elevated to the

status of distinct species, based on experimental tests demonstrating biased intrinsic mating preferences. In these cases, the subsequent claim that hybrids between such entities are the result of interspecific hybridization is largely a semantic argument based on alternative species concepts. Specific examples will be discussed below.

Were the putative parental species correctly identified (or are they identifiable)?

Even if a specimen is an apparent interspecific hybrid, its parentage may be difficult to infer unambiguously. Like luggage at the airport carousel, many *Heliconius* species look alike, and if parentage cannot be unequivocally inferred on the basis of wing pattern, then the "continuum" of exponentially decreasing probability of hybridization with increasing age of divergence proposed by Mallet *et al.* (2007) implies that hypotheses of interspecific hybridization are more parsimonious between more closely-related than more distantly-related species.

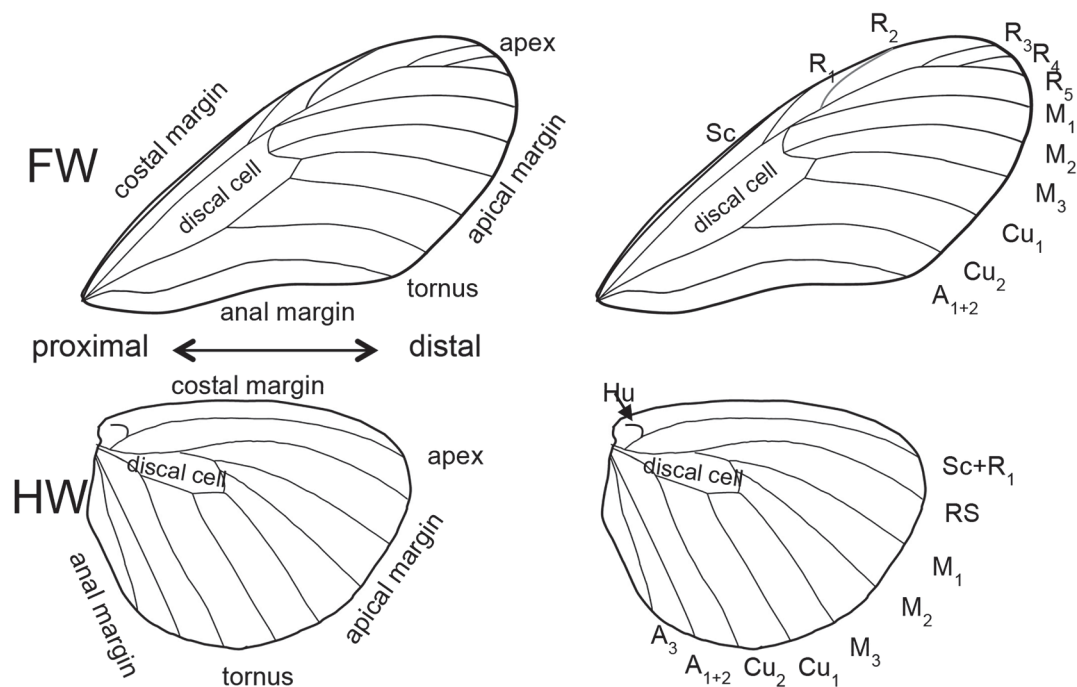


FIGURE 1. *Heliconius* wing regions (left) and venation (right) discussed in the specimen accounts below. Abbreviations: FW = forewing; HW = hindwing; Hu = humeral vein; Sc = subcostal vein; R₁–R₅ = radial veins 1–5; RS = radial sector vein; M₁–M₃ = medial veins 1–3; Cu₁, Cu₂ = cubital veins 1 and 2; A₁₊₂, A₃ = anal veins 1–3. Wing outline modified from Papa *et al.* (2013, fig. 2).

Is the specimen's wing pattern demonstrably "interspecific" in its phenotype, or can it be explained by some other process?

Heliconius wing patterns are composed of multiple, independently-assorting pattern elements (Sheppard *et al.* 1985; Jiggins, 2017). Ideally, a hybrid specimen will exhibit phenotypic characters of both parental forms. That said, given that each instance of hybridization begins with a cross between "typical" parental forms, we would expect most hybrid specimens encountered in the field to be F1 offspring of those parental matings. In many instances, heterozygous F1 individuals result in phenotypes that look like one of the parental forms due to dominance relationships between alternate alleles. Thus, to produce offspring with novel wing patterns, such F1 hybrid individuals need to mate either with one another, or with the "recessive" parental form. Given their rarity, hybrid F1 individuals would be more likely to mate with parental forms than with another hybrid F1, so we would expect to see parental backcrosses before seeing F2 phenotypes. The simple existence of an "atypical" wing pattern that is not clearly a composite of identifiable phenotypic elements coming from the two putative parental forms is not very convincing evidence of hybridization.

Are the hybrid's locality data plausible?

For individuals of two different species to hybridize, they must encounter one another in nature. Interspecific hybrid specimens should therefore have been collected at sites where both parental species (and their particular respective geographical races) are known to co-occur. Vague or dubious locality data on a putative hybrid specimen do not lend credibility to its authenticity. Likewise, inference of a poorly-labeled specimen's provenance and

parentage based on its phenotype is a circular argument that does not provide independent support for the hypothesis of hybrid origin.

Are the specimen's provenance and chain of custody reliable?

As noted previously, (Brower, 2013), *Heliconius* butterflies are valuable commodities in the commercial specimen trade, and the temptation to inflate the value of an unusual specimen by claiming it is "wild-caught" (natural, rather than artificial) is indubitable. Specimens collected in the field by scientists with a known professional reputation, and deposited directly into public collections, are less likely to have false label data than specimens that have been bought, sold or have otherwise changed hands multiple times before being deposited in a museum. It is my default judgment to be skeptical about the provenance of specimens that seem too good to be true, in terms of multiple specimens from the same source, in perfect condition, exhibiting bizarre hybrid phenotypes. This paper documents that many of the ostensible hybrid specimens from collections of European amateurs, including Helmuth and Ruth Holzinger, James Mast de Maeght and Walter Neukirchen, were acquired second- or third-hand by trade or purchase from dealers.

Failure to answer any of the above questions in the affirmative regarding a putative hybrid specimen undermines the credibility of that specimen as evidence for interspecific hybridization in the wild. Reliability scores for each specimen discussed below are assigned as follows: Questions 1-3 are combined into a single identity score, ranging from 0-1, with 1 being certainty that the specimen is indeed an interspecific hybrid. Questions 4 and 5, relating to quality and plausibility of the locality data and other circumstances of the specimen's acquisition are combined into a second authenticity score. The product of these two scores gives a quantitative, albeit subjective, measure of the specimen's relative reliability. Each specimen in the Mallet *et al.* (2007) database, plus some subsequently published hybrids, is scored by this system below. The results are summarized in Table 1 (see Discussion).

The consideration of individual specimens below is formatted as a series of figure legends. Given the quantity of images and the necessity for the reader to refer to them to corroborate the observations and interpretations in the text, this seemed like the most appropriate way to format the main section of the paper. To facilitate the reader's evaluation of the hypothesized parentage of each hybrid, images of the putative parental forms are also presented. Images of all specimens are unaltered from their sources, although in some instances they may be digitally rotated and the background may be cleaned up for uniformity of presentation. Numbering of hybrid specimens follows the numeration in Mallet's online database (<http://www.ucl.ac.uk/taxome/hyb/hybtabs.html>). Label data are transcribed from original labels if the labels were included in the image, and abbreviated terms are expanded for clarity. In some cases, the data labels were not included, in which case the label information was transcribed as reported in the Mallet *et al.* database (<https://bmcevolbiol.biomedcentral.com/articles/10.1186/1471-2148-7-28> 12862_2006_322_MOESM4_ESM.csv). Data considered ambiguous, dubious or unintelligible are followed by a [?].

Collection abbreviations

FLMNH—McGuire Center for Lepidoptera and Research, University of Florida

IAvH—Instituto Alexander Von Humboldt, Bogotá

ICNB—Instituto de Ciencias Naturales, Bogotá

Le Crom—private collection of Jean Francois Le Crom, Bogotá

Mattei—private collection of Mattei family, Venezuela

MNCR—Museo Nacional de Costa Rica

MUSM—Museo de la Universidad de San Marco, Lima

MZPW—Polish Academy of Science, Museum of the Institute of Zoology

NHMUK—Natural History Museum, London

NMS—Naturkunde Museum, Stuttgart

NMW—Naturhistorisches Museum, Vienna

RBINS—Royal Belgian Institute of Natural Sciences

Romero—private collection of the Romero family, Maracay

UCVM—Universidad Central de Venezuela, Maracay

UFRJ—Museum of the Universidade Federal de Rio de Janeiro

UNAM—Museum of the Universidad Nacional Autónoma de México

USNM—Smithsonian, U. S. National Museum of Natural History

Other abbreviations

D—dorsal surface

V—ventral surface

Notes and reliability scores for individual *Heliconius* specimens in the Mallet *et al.* (2007) database

Mallet *et al.* (2007) specimens 1–7 are putative hybrids of the genus *Eueides*, and are not directly pertinent to questions regarding hybridization and gene flow in *Heliconius*. They are ignored for succinctness.

Putative hybrids of various silvaniform *Heliconius* species

The ten species of the silvaniform clade of *Heliconius* (*H. atthis* Doubleday, 1847; *H. besckei* Ménétériés, 1857; *H. elevatus* Nöldner, 1901; *H. ethilla* Godart, 1819 *H. hecale* (Fabricius, 1776); *H. ismenius* Latreille [1817]; *H. luciana* Lichy, 1960; *H. nattereri* C. Felder & R. Felder, 1865; *H. numata* (Cramer, 1780); and *H. pardalinus* Bates, 1862) are for the most part members of the "tiger" mimicry complex with ithomiines in the genera *Melinaea* and *Mechanitis*, with which they share orange or tawny colors and often yellow or white FW distal bands or spots. The monophyly of the silvaniform group and its sister group relationship to the *H. melpomene*-*H. cydno* clade are well-supported (Brower, 1994a; Brower & Egan, 1997; Beltrán *et al.* 2007; Kozak *et al.* 2015; Brower & Garzón-Orduña 2018). A number of the following specimens were interpreted by Mallet *et al.* (2007) as silvaniform x *H. melpomene* hybrids, which would entail inter-clade hybridization events between taxa that diverged in the Pliocene (~4 million years ago; Kozak *et al.* 2015). However, some of these may also be interpreted as intraspecific variants of the highly polymorphic *H. numata*, and others may be interpreted as hybrids between silvaniform species and *H. elevatus*, which is a silvaniform that has converged upon the Amazonian red-rayed mimicry ring. The Figures 2 and 3 exemplify the remarkable mimetic convergence between *H. melpomene* and *H. elevatus*, a source of confusion for predators and biologists alike!



FIGURE 2. *Heliconius melpomene aglaope* C. Felder & R. Felder, 1862 (dorsal; ventral). Peru: Loreto, Contamana, 170 m. 26 May 2002. leg. C. Peña. (Image source: <http://www.tolweb.org/>, images #17224 and #17230). This specimen exhibits a "typical" phenotype of a geographical race with the red forewing "dennis" and hindwing "ray" pattern.



FIGURE 3. *Heliconius elevatus pseudocupidineus* Neustetter, 1931 (dorsal; ventral). Peru: Loreto, Balsapuerto, 220m. Feb. 1919, leg. G. G. Klug. (Image source <http://www.tolweb.org/>, images # 17245 and #17249). *H. elevatus* is a member of the silvaniform clade (as recognized by Eltringham, 1916), and is sister taxon to *H. pardalinus* Bates, 1862. Note that *H. elevatus* bears a yellow subcostal stripe on the HWV, while in rayed *H. melpomene* forms, the corresponding stripe is orange or red. Also note the tendency for the widened proximal end of the red HW rays to exhibit a v-shape, while in *H. melpomene*, they are flat "nail heads."



FIGURE 4. Hybrid #8 (dorsal, ventral). Brazil: Rio Arapiuns [near Santarém], 1980, leg. H. Holzinger[?], Holzinger collection, NMW. Discussed and illustrated in (Holzinger & Holzinger 1994, p. 94; plate 24 fig. 5c). Mallet *et al.* (2007) interpreted this specimen as an *H. numata superioris* (Fig. 5) x *H. melpomene melpomene* (Fig. 6) F1, based on the subapical "red bar" on the forewing. The color of this element appears quite similar, at least in these photographs, to other orange areas of the fore- and hindwings. There are described forms of *H. numata* from Peru with subapical orange markings distal to a yellow band (*H. staudingeri* Weymer, 1894; *H. aristiona staudingeri* f. *lutea* Neustetter, 1931) considered intraspecific hybrid forms of *H. numata* by Lamas & Jiggins (2017). *H. numata mavors* (Fig. 7), which has no yellow bands or spots, occurs in the lower Amazon, along with several other polymorphic forms of *H. numata* with different wing patterns. This specimen could represent an unusual recombinant phenotype of supergene alleles that occur within *H. numata* (Joron *et al.* 2011), or even an *H. numata* x *H. pardalinus* hybrid, which might offer an explanation for the orange chevrons on the HW. Finally, in an obituary for Ruth Holzinger, Aspöck (1996) reported that neither she nor Helmut Holzinger ever ventured outside of Europe. Thus, all of the *Heliconius* specimens in their collection (donated to the Naturhistorisches Museum in Vienna; Lödl *et al.* 1997) were obtained by gift, trade, or purchase from commercial dealers such as Hermann Gerstner.

Identity: 0.1

Authenticity: 0.7

Overall reliability: 0.07



FIGURE 5. *H. numata superioris* Butler, 1875 "typical" form (dorsal, ventral). Brazil: Río Tocantins. (image source: <https://cliniquevetodax.com/Heliconius/pages/numata%20superioris.html>).



FIGURE 6. *H. melpomene melpomene* (Linnaeus, 1758) "typical" form (dorsal, ventral). French Guiana: Route Vidal. (image source: <https://cliniquevetodax.com/Heliconius/pages/melpomene%20melpomene.html>)



FIGURE 7. *H. numata mavors* Weymer, 1894 (dorsal). (image source: <https://cliniquevetodax.com/Heliconius/pages/numata%20mavors.html>)



FIGURE 8. Hybrid #9 (dorsal, ventral). Specimen (in UFRJ) data poor: no date or collector indicated, locality either Obidos or Benjamin Constant, Brazil (approximately 800 miles apart!). Mallet *et al.* (2007) interpreted this specimen as a F1 hybrid between "*H. numata* ?*superioris*" (Fig. 5) and *H. melpomene* nr. *meriana* (Fig. 9). If either locality were correct, it would be unlikely to be related to *H. melpomene meriana*, which does not occur in either place. It is difficult to see an unequivocal contribution from any form of *H. melpomene* to this specimen's phenotype. This could be an intraspecific variant among polymorphic forms of *H. numata*, for example potentially *H. numata arcuella* (Fig. 10) and *H. numata aurora* (Fig. 11), or possibly an *H. numata* x *H. pardalinus* hybrid, as described for Hybrid #8.

Identity: 0.1

Authenticity (due to vague label data): 0.3

Overall reliability: 0.03



FIGURE 9. *H. melpomene meriana* Turner, 1967 "typical" form (dorsal, ventral). French Guiana. (Image source: <https://cliniquevetodax.com/Heliconius/pages/melpomene%20meriana.html>).



FIGURE 10. *H. numata arcuella* Druce, 1874 (dorsal, ventral). Peru: Río Ucayali, Pucallpa, 200 m. (image source: <https://cliniquevetodax.com/Heliconius/pages/numata%20arcuella.html>).



FIGURE 11. *H. numata aurora* Bates, 1862, "typical" form (dorsal, ventral). Peru: Loreto, Iquitos. (image source: <https://cliniquevetodax.com/Heliconius/pages/numata%20aurora.html>). Other variants of this race are more melanic, lacking the yellow apical band on the FW.



FIGURE 12. Hybrid #10 (dorsal; ventral). Brazil: Para, Obidos, 1985. Neukirchen collection (FLMNH). Interpreted by Mallet *et al.* (2007) to be a possible F1 hybrid of *H. numata superioris* Butler, 1875 (Fig. 5) and *H. melpomene* nr. *meriana* (Fig. 9); also suggested to be similar to hybrid #12 (Fig. 15, see below). Presumably the "hybrid" features exhibited by this specimen are the transverse orange bar and the v-shaped marks beneath it on the HW. However, the range of *H. melpomene meriana* does not extend to the Amazon (Rosser *et al.* 2012). It is replaced there by *H. melpomene melpomene* (Fig. 6), which has a red FW band and no markings on the HW. Thus, the hypothesized cross is biogeographically implausible. Furthermore, there are as many as five different forms of *H. numata* co-occurring in the lower Amazon that exhibit most of the features of this specimen (see Hybrid #8). As noted in the introduction, the Neukirchen collection is somewhat problematical as a source of reliable data, as many of its unusual specimens have dubious provenances and were likely purchased from commercial dealers.

Identity: 0.1

Authenticity: 0.8 (collected by an anonymous third party)

Overall reliability: 0.08



FIGURE 13. Hybrid #11 (dorsal; ventral). Peru: Loreto, Río Itaya [near Iquitos]. 1997. Interpreted by Mallet *et al.* (2007) to be an F1 hybrid of *H. numata aurora* (Fig. 11) and *H. melpomene malleti* (Fig. 14), based on wing shape and the FW yellow band. This specimen, apparently collected near Iquitos, Peru by an unnamed third party is in the Neukirchen collection, purchased by the University of Florida's McGuire Center for Lepidoptera and Biodiversity Research (FLMNH). The white marginal dots, the absence of red basal dots, and the v-shaped distal ends of the red rays on the VHW all suggest that a more likely cross would be *H. numata* x *H. elevatus* (e. g., *H. elevatus pseudocupidineus*, Fig. 3). While still interspecific, such a hybrid would be between very closely-related species, rather than more distantly-related members of separate clades.

Identity (corrected): 0.9

Authenticity (due to anonymous collector): 0.75

Overall reliability: 0.675



FIGURE 14. *H. melpomene malleti* Lamas, 1988 (dorsal, ventral). Peru: Loreto. (image source: <https://cliniquevetodax.com/Heliconius/pages/melpomene%20malletti.html>)



FIGURE 15. Hybrid #12 (dorsal; ventral). Guyane: St. Laurent. Holotype of *Heliconius seraphini* Talbot, 1932, from the famous hybrid zone in St. Laurent, French Guiana, collected prior to 1932 (specimen in NHMUK). Interpreted by Ackery and Smiles (1976) as *H. melpomene thelxiope* (Hübner, [1806]) x *H. numata numata*, and interpreted by Mallet *et al.* (2007) to be an F1 hybrid between *H. hecale vetustus* (Fig. 16) and *H. melpomene* interspecific hybrid (*H. melpomene melpomene* (Fig. 6) x *H. melpomene thelxiopeia* (Fig. 17). The locality data suggest that Mallet *et al.*'s parental forms should be preferred. Other than the (probably postmortem) discoloration of the yellow band, the forewing is quite hecale-like. The pointed distal ends of the FW yellow rays and the with of the HW orange rays are reminiscent of *H. melpomene thelxiopeia*. However, the concave proximal edges of the (formerly) yellow FW spots and the presence of rays and submarginal white spots on HWV are more reminiscent of *H. elevatus* (the locally sympatric race is *H. elevatus bari*, Fig. 18) than of *H. melpomene thelxiopeia*. Given the equivocal phenotype, it is more parsimonious to infer a *H. hecale* x *H. elevatus* cross on phylogenetic grounds.

Identity (corrected): 0.9

Authenticity (due to vague label data): 0.9

Overall reliability: 0.81



FIGURE 16. *H. hecale vetustus* Butler, 1873 (dorsal, ventral). French Guiana: Montagne de Kaw Pk 37.5, leg. Y. Lever. (image source: <https://cliniquevetodax.com/Heliconius/pages/hecale%20vetustus.html>)



FIGURE 17. *H. melpomene thelxiopeia* Staudinger, 1897 (dorsal, ventral). French Guiana: Rivière Comte, leg. C. Chazal. Note the reduction of ray elements on the HWV, and rounded proximal edges of yellow spots on FW (image source: <https://cliniquevetodax.com/Heliconius/pages/melpomene%20thelxiopeia.html>).



FIGURE 18. *H. elevatus bari* Oberthür, 1902 (dorsal, ventral). French Guiana: Montagne de Kaw, pk 29.2 (image source: <https://cliniquevetodax.com/Heliconius/pages/elevatus%20bari.html>)



FIGURE 19. Hybrid #13 (dorsal, ventral). Specimen (in UFRJ) data poor: no date or collector indicated, locality either Obidos or Benjamin Constant, Brazil (approximately 800 miles apart!—see also hybrid #9). Mallet *et al.* (2007) interpreted this specimen as a F1 hybrid between "*H. hecale fortunatus*" Weymer, 1883 and *H. melpomene melpomene* (Fig. 6). The name *fortunatus* is a junior synonym of *H. pardalinus radiosus* (Lamas, 2004). (Fig. 20). If from Benjamin Constant, it would be unlikely to be related to *H. melpomene melpomene*, which does not occur there. The dentate HW rays suggest that this is a form of *H. pardalinus*, or possibly a *pardalinus* x *elevatus* cross.

Identity (corrected): 0.5

Authenticity (due to vague label data): 0.3

Overall reliability: 0.15



FIGURE 20. *H. pardalinus radiosus* Butler, 1873 (dorsal). Brazil: Amazonas, Villa Bella [Bolivia:Pando?]. Neukirchen coll. (FLMNH). (image source: <https://cliniquevetodax.com/Heliconius/pages/pardalinus%20radiosus.html>)



FIGURE 21. Hybrid #14 (dorsal, ventral). Colombia: Guainía, Puerto Inírida, 03°52' 16" N, 67°53'31" W, 100m. 14 Jan. 1974, leg. E. Schmidt-Mumm (IAvH). Mallet *et al.* (2007) interpreted this as a potential *H. elevatus zoelleri* (fig. 23) x *H. hecale* backcross to *H. elevatus*, based on the scalloped edge of the hindwing (they suggested that alternatively, it could be a variant of *H. elevatus*, but nevertheless counted it as an interspecific hybrid in their tally). According to Rosser *et al.* (2012), the only other silvaniform occurring at the collection locality is *H. numata aurora* (Fig. 11). This specimen is likely to be just a variant of *H. elevatus*, several other forms of which have yellow subapical spots on the forewing (cf. *H. elevatus bari*, Fig. 18), or the forewing red dennis interrupted by a silvaniform-like black dagger mark (cf. *H. elevatus roraima*, Fig. 23). Keith Willmott (pers. comm.) reports: "I found many mislabeled specimens in Schmidt-Mumm's collection, since, at least the specimens examined, were pinned in the bottom half of a hinged box with the labels separate in the top half. It seems specimens frequently got moved around in the bottom half without their labels also being moved. I have to say this looks like a pretty unusual 'elevatus' variant, and some kind of hybrid origin seems perhaps more likely, but since I would say the label data are highly unreliable, we essentially don't know where it was collected at all. So, difficult to speculate further about a hybrid origin." If the locality data are incorrect, it is possible that the specimen is a *H. elevatus* x *H. pardalinus*.

Identity: 0.2

Authenticity: .75

Overall reliability: 0.15

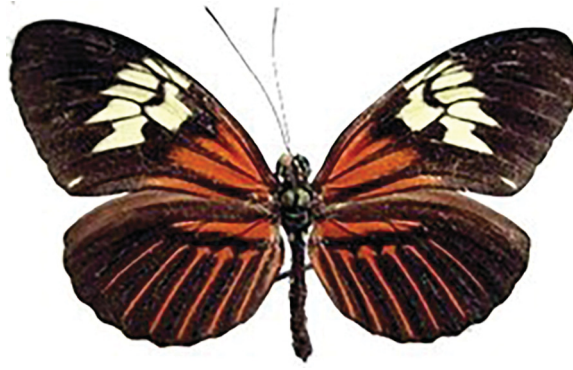


FIGURE 22. *H. elevatus zoelleri* Neukirchen, 1990 (dorsal). Venezuela: Amazonas, Puerto Ayacucho. R. Mattei coll. (image source: <https://cliniquevetodax.com/Heliconius/pages/elevatus%20zoelleri>). Note the scalloped edges of the wings.



FIGURE 23. *H. elevatus roraima* Turner, 1966 (dorsal, ventral). Venezuela: Bolivar, Via Roraima km 7. (image source: <https://cliniquevetodax.com/Heliconius/pages/elevatus%20roraima>).



FIGURE 24. Hybrid #15 (dorsal, ventral). Peru: Loreto, Yurimaguas, collected in July, 1919 by O. Michael. Currently housed in the Holzinger collection in NMW. This specimen is the holotype of *H. elevatus* f. *nöldneri* Neustetter, 1938. Mallet *et al.* (2007) interpreted this as a F1 *H. elevatus pseudocupidineus* (Fig. 3) x *H. hecale versicolor* Weymer 1894 (a synonym of *H. hecale felix*, Fig. 25), backcross, presumably based on the orange patches at the base of the FW yellow band and at the outer margin of the FW.

Identity: 0.9

Authenticity: 0.75

Overall reliability: 0.675



FIGURE 25. *H. hecale felix* Weymer, 1894 (dorsal, ventral). Bolivia: Yungas, Caranavi. (image source: <https://cliniquevetodax.com/Heliconius/pages/hecale%20felix.html>)



FIGURE 26. Hybrid #16 (dorsal). Bolivia: Chaparé, Todos Santos, 1969, coll. H. Holzinger (NMW). Interpreted by Mallet *et al.* (2007) as F1 of *H. hecale zeus* Neukirchen, 1995 (= *H. hecale felix* according to Rosser *et al.* 2012, Fig. 25) x *H. elevatus perchlora* (Fig. 27). I concur with Mallet *et al.*'s view that this could be a hybrid between *H. elevatus* and another silvaniform—*H. numata mirus* (Fig. 28) or *H. pardalinus ariadne* Neukirchen, 1995 (see image at http://www.butterfliesofamerica.com/L/ih/heliconius1316_i.htm) are other possible parents.

Identity: 0.9

Authenticity: 1.0

Overall reliability: 0.9



FIGURE 27. *H. elevatus perchlora* Joicey & Kaye, 1917 (dorsal, ventral). Bolivia: "Route de Cochabamba" F. Coenen coll. (image source: <https://cliniquevetodax.com/Heliconius/pages/elevatus%20perchlora>)



FIGURE 28. *H. numata mirus* Weymer, 1894 (dorsal, ventral). Bolivia: La Paz, Caranavi. (image source: <https://cliniquevetodax.com/Heliconius/pages/numata%20mirus.html>)



FIGURE 29. Hybrid #17 (dorsal, ventral). No locality data (NHMUK). Ackery and Smiles (1976) and Brown (1976) suggested this specimen, the holotype of *H. hippola* Hewitson, 1867, could be a hybrid between *H. ethilla metalilis* Butler, 1873 (Fig. 30) and *H. melpomene melpomene* (Fig. 6). Mallet *et al.* (2007) accepted that interpretation and inferred the locality to be "?Colombia", presumably based on the distributions of the two putative parental forms and similarity to Hybrid #18 noted by Brown. However, the specimen could be any silvaniform, many forms of which are orange and black with no yellow spots, and it is hard to see any conclusive contribution from any form of *H. melpomene* in this phenotype.

Identity: 0.2

Authenticity: 0.2

Overall reliability: 0.04



FIGURE 30. *H. ethilla metalilis* Butler, 1873 (dorsal, ventral). Venezuela: Bolivar. (image source: <https://cliniquevetodax.com/Heliconius/pages/ethilla%20metallitis.html>). According to Brown (1976), specimens of *H. ethilla* can often be diagnosed by the presence of a small red basal spot on the HWV between the cubital and anal veins.



FIGURE 31. Hybrid #18 (dorsal, ventral). Colombia: Meta, Villavicencio, Rio Negro, 04°12'00 N, 73°42'23"W, 1200m, 10 Feb.(?) 1970. leg. E. Schmidt-Mumm (IAvH). Interpreted by Brown (1976) and Mallet *et al.* (2007) as an F1 *H. ethilla* nr. *metalilis* x *H. melpomene melpomene*, like #17. The *H. ethilla* form that occurs in Villavicencio is now called *latona* (Fig. 32). Although the diagnostic red HWV spot is present, as with #17, there is little to suggest that this specimen is a result of hybridization with *H. melpomene*. It could represent a hybrid with a form of *H. numata*, which is polymorphic in that region (cf. Fig. 33). As a Schmidt-Mumm specimen, the locality data are also potentially suspect (see Hybrid #14).

Identity: 0.3

Authenticity: 0.8

Overall reliability: 0.24



FIGURE 32. *H. ethilla latona* Neukirchen, 1998 (dorsal, ventral). Colombia: Meta, Villavicencio, leg. G. Nielsen. (image source: <https://cliniquevetodax.com/Heliconius/pages/ethilla%20latona.html>).



FIGURE 33. *H. numata bicoloratus* Butler, 1873 (dorsal, ventral). Ecuador: [Pastaza?], Santa Clara, Cabanas Platua. (image source: <https://cliniquevetodax.com/Heliconius/pages/numata%20bicoloratus.html>). One of several sympatric polymorphic forms occurring in the upper Amazon basin.



FIGURE 34. Hybrid #19 (dorsal, ventral). Colombia: Meta, Cubarral, 1979, leg. E. Schmidt-Mumm (IAvH). Interpreted by Mallet *et al.* (2007) as *H. melpomene melpomene* (Fig. 6) x *H. ethilla* nr. *metalilis* (Fig. 30) F1 backcross to *H. ethilla*. Presumably, the basis for this interpretation is the area of brownish scales apical to the yellow FW band, but many silvaniforms, including some races of *H. ethilla*, exhibit brown or tawny scales in the forewing apex. There do not appear to be any other characters suggesting a hybrid origin for this specimen. Note also the potential mislabeling problems reported by K. Willmott (see Hybrid #14).

Identity: 0.2

Authenticity: 0.8

Overall reliability: 0.16



FIGURE 35. Hybrid #20 (dorsal, ventral). Colombia: Meta, Cubarral, 03°47'43"N, 73°50'36"W, 800 m., 31 Dec. 1979, leg. E. Schmidt-Mumm (same data as #19?), (IAvH). Another specimen interpreted by Mallet *et al.* (2007) as a *H. melpomene melpomene* (Fig. 6) x *H. ethilla* nr. *metalilis* (Fig. 30) F1 backcross to *H. ethilla*. The reddish basal spot in CU2 of HWV is diagnostic of *H. ethilla*. Note significant differences in multiple pattern elements between this specimen and #19, including presence vs. absence of HW marginal white spots, pattern of black spots on FW, etc. The reddish brown/yellow interface of the distal forewing band separated by a line of black scales is vaguely reminiscent of the forewing pattern of *H. heurippa* (Fig. 148), but the angle of the bands across the wing is quite different. The sharp distal boundary of the FW yellow bar with reddish brown (not red, as in *H. melpomene*) scales beyond it is suggestive of a hybrid phenotype. However, there is once again a potential mislabeling problem, as reported by K. Willmott (see Hybrid #14).

Identity: 0.6

Authenticity: 0.8

Overall reliability: 0.48



FIGURE 36. Hybrid # 21 (dorsal, ventral). Venezuela: Barinas, Barinitas, (no date or collector), O. Mattei collection. Interpreted by Mallet *et al.* (2007) as a *H. numata peeblesi* (Fig. 37) X *H. ethilla metalilis* (Fig. 30) F1 hybrid, without further explanation. This specimen has thicker medial and marginal black bands on the HW than either of the putative parental forms, but otherwise is quite numata-like. There MAY be a basal red spot on HWV, suggestive of *H. ethilla*, but the image is of insufficient quality to be certain. It is not clear what other features suggest it to be of hybrid origin.

Identity: 0.2

Authenticity: 0.9

Overall Reliability: 0.18



FIGURE 37. *H. numata peeblesi* Joicey & Talbot, 1925 (dorsal, ventral). Venezuela: Barinas. (Image source: <https://cliniquevetodax.com/Heliconius/pages/numata%20peeblesi.html>).



FIGURE 38. Hybrid #22 (dorsal, ventral). Brazil: Espirito Santo, Santa Leopoldina (or Minas Jerais, Leopoldina), prior to 1908, from the Riffarth collection (NHMUK). Mallet *et al.* (2007) followed Brown (1976) in interpreting this as a potential F1 between *H. ethilla narcaea* (Fig. 39) and *H. numata ethra* (Fig. 40). Neither offered any explanation of the characters leading to their determination. *H. ethilla* from southeastern Brazil typically has a single roundish white apical spot on the forewing, while *H. numata* has a broken yellow band or row of three yellow spots. This specimen has a row of whitish spots. The medial yellow forewing band of this specimen is similar to that of *H. ethilla*. Thus, perhaps it is a hybrid.

Identity: 0.9

Authenticity: 0.7 (due to vagueness of data)

Overall reliability: 0.63



FIGURE 39. *H. ethilla narcaea* Godart, 1819 (dorsal, ventral). Brazil: Santa Catarina. (image source: <https://cliniquevetodax.com/Heliconius/pages/ethilla%20narcaea.html>).



FIGURE 40. *H. numata ethra* (Hübner, [1831]) (dorsal, ventral). Brazil: Pernambuco, São Lourenço da Mata, coll. M. Demaio. (image source: <https://cliniquevetodax.com/Heliconius/pages/numata%20ethra.html>)



FIGURE 41. (dorsal, ventral). Hybrid specimen not included in Mallet *et al.* (2007). Peru, Rio Ucayali, Contamana, Oct. 2008, ex Bueche. Image source: <http://www.heliconius.org/2013/two-more-heliconius-hybrids/> This specimen could be a dark *H. pardalinus* form (cf. Fig. 42), or perhaps a *H. pardalinus* x *H. elevatus pseudocupidineus* (compare forewing band of Fig. 3). According to the cited web page, Mallet apparently believed this specimen to be wild caught. However, the indicated source, Martin and Beatrice Bueche, are owners of Jardin du Papillons, in Hunawihr, Alce, France, a butterfly house with captive *Heliconius*. See <http://www.jardinsdespapillons.fr/>

Identity: 0.5

Authenticity: 0.0

Overall Reliability: 0.0



FIGURE 42. *H. pardalinus tithoreides* Staudinger, 1900 (dorsal). Peru: San Martín. A. Cahurel coll. (image source: <https://cliniquevetodax.com/Heliconius/pages/pardalinus%20tithoreides.html>)



FIGURE 43. (dorsal, ventral). Hybrid specimen not included in Mallet *et al.* (2007). Ecuador: Morona-Santiago, Puerto Morona, Sept., 2011, leg. K. Willmott? (K. Willmott pers. comm. says that he was not the collector, and that Ismael Aldaz probably was, and that the locality data are reliable). Image source <http://www.heliconius.org/2013/two-more-heliconius-hybrids/>

Apparently wild-caught. The white marginal spots and chevron-shaped rays on the hindwing suggest that this is specimen is likely a *H. pardalinus* ssp. x *H. elevatus pseudocupidineus* (Fig. 3) hybrid. See Hybrid #11 (Fig. 13) and Hybrid #12 (Fig. 15), above. Phenotypically, *H. pardalinus julia* (Fig. 44) would seem like a plausible parent, but K. Willmott (pers. comm.) says that form does not occur at the collection locality. Although Rosser *et al.* (2012) do not indicate any records of *H. pardalinus* in southern Ecuador, possible alternative races are *H. pardalinus butleri* Brown, 1976 or *H. pardalinus dilatus* Weymer, 1894.

Identity: 0.9

Authenticity: 0.9

Overall Reliability: 0.81



FIGURE 44. *H. pardalinus julia* Neukirchen, 2000 holotype (dorsal). Ecuador, Sucumbios, Laguna de Pañachocha, Rio Pañayacu, 250 m. 12–14.Oct. 1997. leg. K. Willmott (NHMUK) (image source: <https://cliniquevetodax.com/Heliconius/pages/pardalinus%20julia.html>)

Putative hybrids between *H. ethilla narcaea* and *H. besckei*

This series of six specimens are all ostensibly from southeastern Brazil, where the two parental species are sympatric. Both belong to the silvaniform clade, although *H. besckei* has converged upon the mimetic pattern of sympatric *H. melpomene nanna* Stichel, 1899 and *H. erato phyllis* (Fabricius, 1775). The locality and collector data are of variable quality, but the specimens themselves are for the most part in pristine condition. The excellent condition is itself a cause for suspicion about these butterflies' origins from the wild.



FIGURE 45. Hybrid #23 (dorsal). Brazil: Rio Grande do Sul (or Santa Catarina) (two adjacent states in southern Brazil). No further locality data indicated. Specimen housed in the Holzinger collection in MNW, obtained by the Holzingers from Hermann Gerstner, a commercial butterfly dealer in Schweinfurt, Germany. Interpreted by Mallet *et al.* (2007) as an F1 of *H. ethilla narcaea* (Fig. 39) x *H. besckei* (Fig. 46). The reddish forewing band (and absence of round, white apical spot typical of *narcaea*) is certainly suggestive of a hybrid specimen. Fine condition and commercial origins suggest that the specimen was reared for the trade.

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09



FIGURE 46. *H. besckei* Ménétriés, 1857 (dorsal, ventral). Brazil. Note the red marginal stripe on HWV, which is the diagnostic character of this species. (image source: <https://cliniquevetodax.com/Heliconius/pages/beskei.html>)



FIGURE 47. Hybrid #24 (dorsal, ventral). Brazil: Santa Catarina, Joinville, 1985. In the Neukirchen collection, (FLMNH). Interpreted by Mallet *et al.* (2007) as an F1 of *H. ethilla narcaea* (Fig. 39) x *H. besckei* (Fig. 46). This specimen is very similar to #23 (Fig. 45) in its fine condition and vague locality data, suggesting that Neukirchen could have purchased it from a dealer, and that it could have been bred in captivity for the commercial trade.

Identity: 0.9

Authenticity: 0.2

Overall reliability: 0.18



FIGURE 48. Hybrid #25 (dorsal, ventral). Brazil: Santa Catarina, Joinville, 1981, leg. H. Miers. Collection "Para" ((Museu Paraense Emilio Goeldi?). Interpreted by Mallet *et al.* (2007) as an F1 of *H. ethilla narcaea* (Fig. 39) x *H. besckei* (Fig. 46). Herbert W. Miers was a serious amateur lepidopterist in Joinville, which lends more credibility to this specimen's authenticity than the vague provenance of the previous two. It is notable that this specimen, as well as the next two, are from the same museum.

Identity: 0.9

Authenticity: 0.9

Overall reliability: 0.81



FIGURE 49. Hybrid #26 (dorsal, ventral). Brazil: Rio de Janeiro, Imbarie, 1963, leg. H. Ebert. Collection "Para" (Museu Paraense Emilio Goeldi?). Interpreted by Mallet *et al.* (2007) as an F1 of *H. ethilla narcaea* (Fig. 39) x *H. besckei* (Fig. 46). Heinz Ebert was a serious amateur lepidopterist from Rio Claro, SP, Brazil.

Identity: 0.9

Authenticity: 0.9

Overall reliability: 0.81



FIGURE 50. Hybrid #27 (dorsal, ventral). Brazil: Santa Catarina, Agrolandia, prior to 1997, leg. H. Wulff. Collection "Para" (Museu Paraense Emilio Goeldi?). Interpreted by Mallet *et al.* (2007) as an F1 of *H. ethilla narcaea* (Fig. 39) x *H. besckei* (Fig. 46).

Identity: 0.9

Authenticity: 0.9

Overall reliability: 0.81



FIGURE 51. Hybrid #28 (dorsal, ventral). Brazil: Sao Paulo, Horto Forestal, 1947 (MNW). Interpreted by Mallet *et al.* (2007) as a backcross to *H. besckei* (Fig. 46) of an *H. ethilla narcaea* (Fig. 39) x *H. besckei* F1. Mallet *et al.* (2007) indicated Helmuth Holzinger as the collector. However, as noted under Hybrid #8, the Holzingers did not capture any *Heliconius* themselves. It is likely that the specimen was purchased.

Identity: 0.9

Authenticity: 0.5

Overall reliability: 0.45

Putative hybrids between various races of *H. cydno* Doubleday, 1847 and *H. melpomene* (L., 1758)

This series of specimens represents some of the most important evidence supporting hypotheses of interspecific gene flow and homoploid hybrid speciation in *Heliconius*. There is now quite strong quantitative evidence that various races of *H. melpomene* and *H. cydno* are completely reproductively isolated from one another (Garzón-Orduña and Brower, 2017).

Putative Central American *H. melpomene* x *H. cydno* hybrids

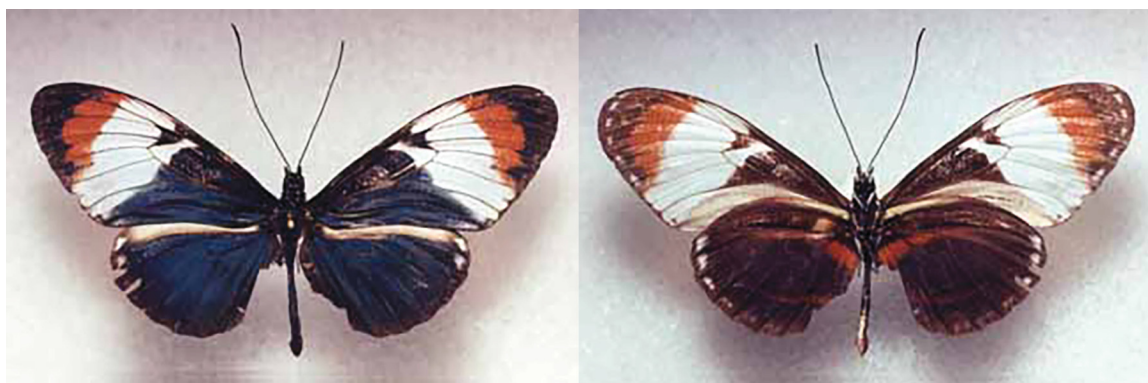


FIGURE 52. Hybrid #29 (dorsal, ventral). Costa Rica, Río Sarapiquí, 600m. 12 Feb. 1993. leg. M. Posla-Fuentes.



FIGURE 53. Hybrid #30 (dorsal, ventral). Costa Rica, Río Sarapiquí, 600m. 4 Feb. 1993. leg. M. Posla-Fuentes. Not illustrated in the Mallet *et al.* (2007) supplementary information. Image source http://www.troplep.org/TL_abstracts12.html#MAY%201993%20Volume%204,%20Number%201 (freely available on line).



FIGURE 54. *Heliconius cydno galanthus* Bates, 1864 "typical" phenotype, dorsal and ventral surfaces. Costa Rica: Chirripo, Paso Marcos. (Image source <https://cliniquevetodax.com/Heliconius/pages/cydno%20galanthus.html>)



FIGURE 55. *Heliconius melpomene rosina* Boisduval, 1870 "typical" phenotype, dorsal and ventral surfaces. Costa Rica: Chirripo, Paso Marcos. (Image source <https://cliniquevetodax.com/Heliconius/pages/melpomene%20rosina.html>)

Both Hybrid #29 and #30 were interpreted by Mallet *et al.* (2007) as *H. cydno galanthus* (Fig. 54) x *H. melpomene rosina* (Fig. 55) F1 backcross to *H. cydno galanthus*. Hybrid #29, but apparently not Hybrid #30, is in the MNCR.

There are several observations to be made regarding the credibility of Hybrids # 29 and 30. The collector, Mario Posla-Fuentes, published illustrations of the two specimens and brief notes in two separate articles (Posla-Fuentes 1993a, b). Posla's address is listed as "Butterfly Paradise" on one, and ENTOCOS on the other, and in both, he indicated that he had a greenhouse with *Passiflora*, upon which Hybrid #30 laid 7 eggs. This suggests that Posla had access to a butterfly rearing facility. While there is no *prima facie* reason to doubt his word that the specimens were captured in the wild, he does not have a reputation one way or another as a known scientist or collector. The poor condition of the specimens is consistent with their having been alive for some period of time before they were killed (although antennal breakage is likely due to rough handling postmortem). If they were indeed wild-caught, given the same locality and temporal proximity of the reported capture dates, it is likely that the two specimens are siblings from the same hybridization event.

Regarding the specimens themselves, the phenotypes of the two are remarkably similar, with mostly *cydno*-like characters, including a broad FW white band with the "hourglass" mark in the end of the discal cell, white HW submarginal spots, and HWV brown "forceps." The only atypical feature is the brownish-red band distal to the white in the forewing.

A lab-reared F1 of *H. melpomene rosina* x *H. cydno chioneus*, both from Panama, is shown in Fig. 56. Although the width of the HW band differs between *H. cydno galanthus* and *H. cydno chioneus*, the forewing bands of the two races are similar (the former is slightly more extensive distally), so the comparison is germane. As may be seen, the lab-reared hybrid's white FW band is much narrower than those of Hybrids #29 and #30, and does not reach the outer margin of the wing. The white "hourglass" in the end of the FW discal cell is incomplete in the lab-reared F1, but complete in hybrids #29 and #30. The position of the red band is more proximal, and the boundary between the red and white is a more or less straight line in the lab-reared F1, while in Hybrids # 29 and #30 it is convex towards the wing apex. Also note the partial suppression of the HWV "forceps" in the lab-reared F1 below. It is likely due to these phenotypic differences that Mallet *et al.* (2007) interpreted specimens #29 and #30 to be backcrosses to *H. cydno*.

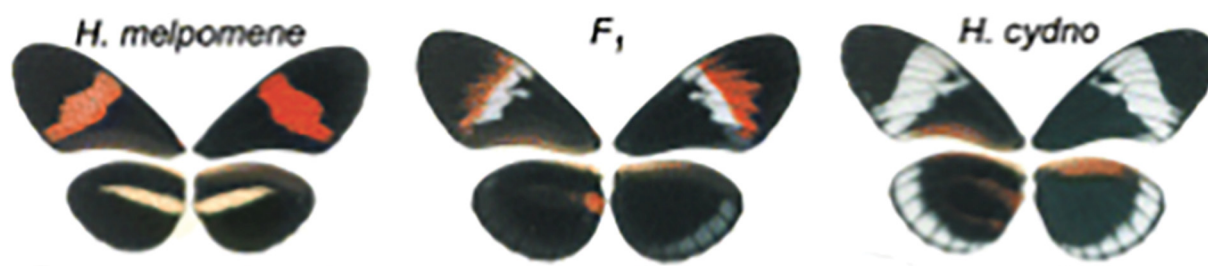


FIGURE 56. Parental forms (left, right) F1 (center) from laboratory cross between *H. melpomene rosina* and *H. cydno chioneus* from central Panama (Naisbit *et al.* 2003, their Fig. 1, in part—open access DOI: 10.1046/j.1525-142X.2003.03034.x). Left pair of wings for each form is ventral surfaces, right pair is dorsal surfaces.

In the forewings of F1 backcrosses performed in the lab by Naisbit *et al.* (2003) (Fig. 57), the white band never reaches the outer margin of the forewing when there is a distal red band present, nor is the white "hourglass" in the discal cell complete, both characters which differ from the pattern expressed in Hybrids #29 and #30.



FIGURE 57. Variability in pattern of white and red bands on forewing in *H. melpomene rosina* x *H. cydno chioneus* backcrosses (Naisbit *et al.* 2003, their Fig. 1, in part).

Gilbert (2003) illustrated a number of "synthetic" (i. e., reared under loosely-controlled conditions in the greenhouse atop the University of Texas biology building) *H. melpomene*-*H. cydno* hybrids with forewing bands that look more like #29 and #30 (e. g., his Plate 14.1 fig. 14.1h and Plate 14.4 lower-middle panel d), but their red coloration is "bright rose-pink," not "red-brown." In sum, the wing patterns of specimens #29 and #30 are not identical to those of any published *H. melpomene*-*H. cydno* lab-reared hybrid. Further, given the diversity of wing patterns expected in an F1 backcross, it would be extremely unlikely to capture two virtually identical specimens from among the diverse hybrid phenotypes expected from such a cross.

Alternatively, we know that *H. cydno* (and its allopatric cognates) and *H. melpomene* are recently-diverged sister taxa in which wing patterns have evolved extremely rapidly, and that red forewing pattern elements are a symplesiomorphic trait for the clade (Brower, 2011). It is not implausible to hypothesize a mutation in the germ line of the B locus that led to atavistic expression of a distal red-brown band (as seen in *H. heurippa*, Fig. 148).

Identity (Hybrid #29 and Hybrid #30): 0.3

Authenticity: 0.75

Overall reliability: 0.225



FIGURE 58. Hybrid #31 (dorsal, ventral). Costa Rica: Limón, Guácimo, San Luis, 2001, leg. T. Fox. Specimen in the NHMUK. Interpreted by Mallet *et al.* (2007) as a *H. cydno galanthus* (Fig. 54) x *H. melpomene rosina* (Fig. 55) F1. Given the discussion above, the expression of the HWV forceps pattern and wide red FW band suggest that this is not an F1 (although the orange-red color of the forewing band is more *melpomene*-like than the brownish coloration of the distal band in the previous two "hybrids." Despite the unorthodox spreading of the specimen, it appears to be in mint condition. There is no information available about the collector, and there are now many specimens like this one being produced in butterfly houses, as may be observed in the results of a Google image search for "*Heliconius heurippa*."

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09



FIGURE 59. Hybrid #32 (dorsal, ventral). Panama: Pipeline Road, 1979. Leg. Gross, specimen housed in USNM. Interpreted by Mallet *et al.* (2007) as a *H. melpomene rosina* (Fig. 55) x *H. cydno chioneus* (Fig. 60) F1 backcross to *H. cydno chioneus*. Other than the broad white HW band characteristic of *H. cydno chioneus*, this specimen is very similar in its phenotype to Hybrids #29 and #30, and the same questions arise regarding its ancestry.

Identity: 0.5

Authenticity: 0.9

Overall reliability: 0.45



FIGURE 60. *H. cydno chioneus* Bates, 1864 (dorsal). Panama, M. Demaio coll. (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20chioneus.html>)

Putative hybrids between *H. melpomene cythera* and *H. cydno alithea*

These two races are sympatric on the western slope of the Andes in Ecuador. *H. melpomene cythera* (Fig. 61) is comimetic with *H. erato cyrbia* Godart, 1819. *H. cydno alithea* (Figs. 62, 63) is dimorphic: a yellow morph is comimetic with *H. eleuchia primularis* Butler, 1869, and a white morph is comimetic with *H. sapho candidus* Brown, 1976.



←
FIGURE 61. *H. melpomene cythera* Hewitson, 1869 (dorsal, ventral). Ecuador [Pacific slope of Andes]. (image source: <https://cliniquevetodax.com/Heliconius/pages/melpomene%20cythera.html>) Note the transverse yellow HW bar is expressed only on the ventral surface. Also, note that the marginal HW white scales are separated by dark scales on the veins, and that the inner margin of these markings within each wing cell is u-shaped.



FIGURE 62. *H. cydno alithea* Hewitson, 1869 (yellow form, dorsal, ventral). Ecuador: Esmeraldas, Region de Lita, Chuchuvi. (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20alithea>). Note that the HW yellow (or white) marginal band extends proximally so that it almost entirely obscures the distal brown forceps mark (thus filling approximately 1/3 of the entire wing area). Also note that within each HW cell, the inner margin of this band is m-shaped, with two white or yellow lobes extending towards the wing base, with a line or v-shaped group of dark scales running down the center of each cell towards the margin.



FIGURE 63. *H. cydno alithea* Hewitson, 1869, form ""neustetteri"" Riffarth, 1908 (dorsal). Ecuador: Esmeraldas. This is the white form, lacking hourglass mark in FW discal cell. See Kapan (2001) for details of this polymorphism.





FIGURE 64. Hybrid #33 (dorsal, ventral). Holotype of *Heliconius vulcanus* f. *concinna* Stichel, 1906. Ecuador: Bolivar Prov., Balzapamba. Specimen collected by (or sold to Stichel by) Richard Haensch (a Berlin insect dealer who collected in Ecuador in 1899–1900), now housed in the NHMUK. Interpreted by Ackery & Smiles (1976) as a form of *H. melpomene cythera* (Fig. 61), and by Mallet *et al.* (2007) as a *H. cydno alithea* (Fig. 62) x *H. melpomene cythera* F1 backcross to *H. melpomene*. Typical pattern elements present in either the yellow or white forms of *H. cydno alithea* include a HWV brown forceps pattern, a much broader white (or yellow) HW band with m-shaped pattern elements, and often an hourglass mark in the FW discal cell. This specimen does not exhibit any of those features. Experimental crosses of *H. melpomene cythera* and *H. melpomene melpomene* (Fig. 6) from French Guiana by Jiggins *et al.* (2005) (Fig. 65) clearly reveal that the yellow markings on the proximal part of the forewing band, the white submarginal spots on the forewing, the indistinct yellow band on the HWV, and yellow scales in the HW marginal band all represent phenotypic variation already present in *H. melpomene*. Since none of these yellow or white pattern elements appear in French Guianan *H. melpomene melpomene*, the implication is that they must represent latent variability in *H. melpomene cythera*. If that is true, there is no reason to invoke interspecific hybridization to explain this specimen's atypical pattern. It is more parsimonious to interpret it as a variant of *H. melpomene cythera*.

Identity (as an interspecific hybrid): 0.1

Authenticity: 1.0

Overall reliability: 0.1

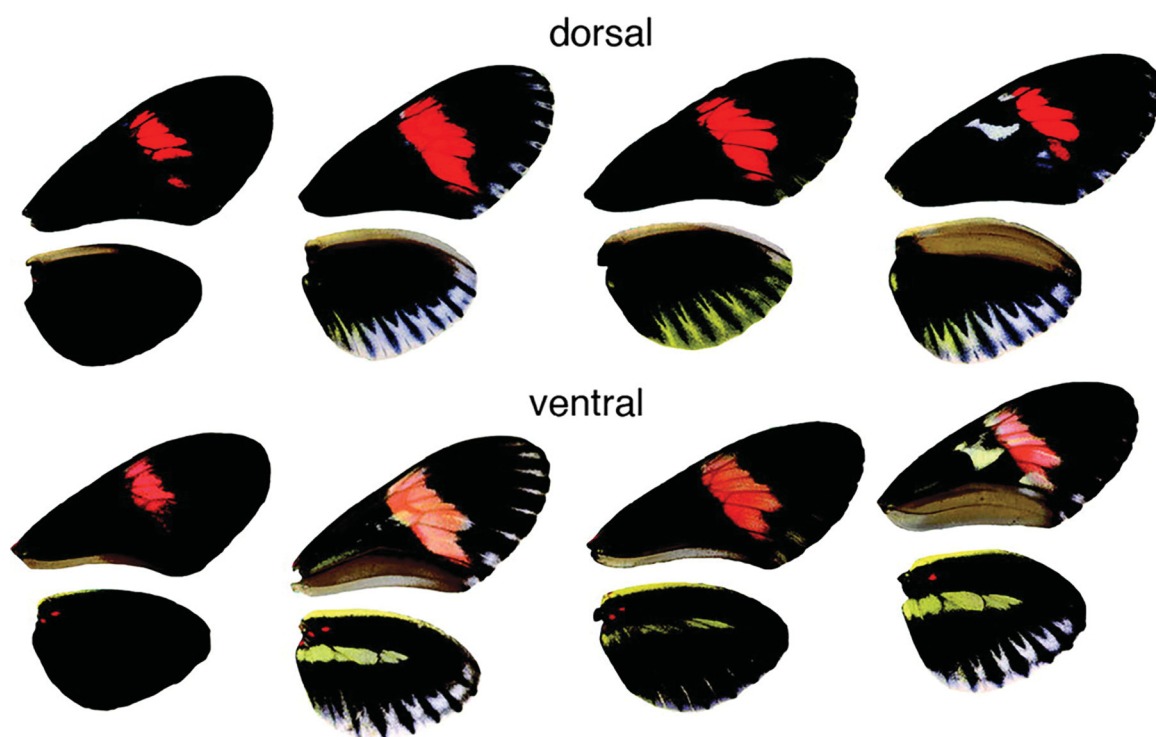


FIGURE 65. Intraspecific laboratory crosses of *H. melpomene cythera* and *H. melpomene melpomene* from Jiggins *et al.* (2005, open access). Note the expression of white/yellow pattern elements in the forewing band, and yellow scales in the HW submarginal band.





FIGURE 66. Hybrid #34 (dorsal, ventral). Ecuador, Los Ríos, Río Palenque, 1973, leg. C. Dodson, housed in FLMNH. Interpreted by Mallet *et al.* (2007) as a *H. melpomene cythera* (Fig. 61) x *H. cydno alithea* (Fig. 62) F1. The specimen has typical markings of a white "neustetteri" form *H. cydno alithea*, except for the distal reddish scales on the forewing. The color, shape and location of this patch of scales are different from the pinkish scales on *H. melpomene cythera*, which form a clearly-defined, narrow band across the end of the discal cell. However, they are reminiscent of the *H. melpomene rosina* x *H. cydno chioneus* F1 shown in Fig. 56 (not that the brown HWV forceps appears to be completely expressed in this specimen, which is not likely to occur in an F1).

Identity: 0.5

Authenticity: 1.0

Overall reliability: 0.5



FIGURE 67. Hybrid #35 (dorsal, ventral). Ecuador: Pichincha, Alluriquin, 850 m. 1989, leg. C. Callegari, housed in MUSM. Interpreted by Mallet *et al.* (2007) as a *H. melpomene cythera* (Fig. 61) x *H. cydno alithea* (Fig. 62) F1. Similar to Hybrid #34, except that the brown HWV forceps is reduced to a basal mark. Also, the discal cell hourglass mark is partly expressed on the FWV.

Identity 0.9

Authenticity: 1.0

Overall reliability: 0.9



FIGURE 68. Hybrid #36 (dorsal, ventral). Ecuador: Palmar, 100 m. Specimen collected by (or sold to Stichel by) Richard Haensch (a Berlin insect dealer who collected in Ecuador in 1899–1900), now housed in the NHMUK. Interpreted by Mallet *et al.* (2007) as *H. melpomene cythera* (Fig. 61) x *H. cydno alithea* (Fig. 62) F1 backcross to *H. melpomene cythera*, presumably on the basis of the white scales on the proximal edge of the forewing band. The pattern may be interpreted as Hybrid #33.

Identity: 0.1

Authenticity: 0.9

Overall reliability: 0.09



FIGURE 69. Hybrid #37 (dorsal, ventral). Ecuador: Palmar, 100 m. Specimen collected by (or sold to Stichel by) Richard Haensch (a Berlin insect dealer who collected in Ecuador in 1899–1900), now housed in the NHMUK. Interpreted by Mallet *et al.* (2007) as *H. melpomene cythera* (Fig. 61) x *H. cydno alithea* (Fig. 62) F1 backcross to *H. melpomene cythera*, presumably on the basis of the white scales on the proximal edge of the forewing band. The yellow HWV stripe is also only faintly visible (an *H. melpomene* trait seen in intraspecific hybrid zones in eastern Panama). The pattern may be interpreted as Hybrid #33.

Identity: 0.1

Authenticity: 0.9

Overall reliability: 0.09

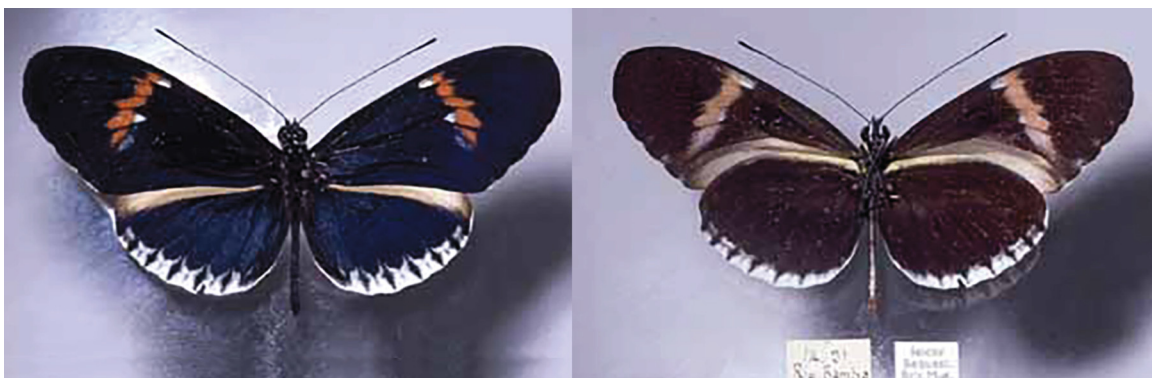


FIGURE 70. Hybrid #38 (dorsal, ventral). Ecuador: Riobamba, "1931. leg. Joicey." This locality was likely the point of shipment to Europe, rather than the collection locality, as Riobamba is above 2700m in the Andes and therefore not *Heliconius* habitat. The specimen is likely another Richard Haensch specimen, sent to Stichel or Riffarth, which came to the NHMUK via the Joicey bequest in 1931. Interpreted by Mallet *et al.* (2007) as *H. melpomene cythera* (Fig. 61) x *H. cydno alithea* (Fig. 62) F1 backcross to *H. melpomene cythera*, presumably on the basis of the white scales on the proximal edge of the forewing band. The yellow HWV stripe is also only faintly visible (an *H. melpomene* trait seen in intraspecific hybrid zones in eastern Panama). The pattern may be interpreted as Hybrid #33.

Identity: 0.1

Authenticity: 0.5 (poor data)

Overall reliability: 0.05



FIGURE 71. Hybrid #39 (dorsal). Ecuador: Pichincha, San Miguel de los Bancos, 1993, leg. D. Kapan. Interpreted by Mallet *et al.* (2007) as *H. melpomene cythera* (Fig. 61) x *H. cydno alithea* (Fig. 62) F1 backcross to *H. melpomene cythera*, presumably on the basis of the white scales on the proximal edge of the forewing band and white marginal spots on the forewing. The pattern may be interpreted the same as Hybrid #33. This specimen is notable as one of the few putative interspecific hybrids collected by a professional *Heliconius* biologist. Kapan collected a second specimen (Ecuador: Pichincha, El Padrino, 1994) (Hybrid #40) which Mallet *et al.* (2007) did not illustrate. Presumably it is similar to #39, and both are given the same scores here.

Identity: 0.0

Authenticity: 1.0

Overall reliability: 0.0

Putative *H. cydno cydno* x *H. melpomene martinae* hybrids

The following specimens are all viewed to be hybrids between races of *H. melpomene* and *H. cydno* endemic to the Magdalena Valley in central Colombia.



FIGURE 72. *H. cydno cydno* Doubleday, 1847 (dorsal, ventral). Colombia [Magdalena Valley] (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20cydno.html>)



FIGURE 73. *H. melpomene martinae* Cast & Le Crom, 2012 (dorsal, ventral). Colombia: Boyacá, Otanche. Sheppard *et al.* (1985) and subsequent authors used the name *euryas* Boisduval, 1870 for the race of *H. melpomene* from the Magdalena Valley in Colombia. Lamas (2004) noted that the name *euryas* correctly applies to the local form of *H. erato*, and is therefore a junior synonym of *H. erato guarica* Reakert, 1868 (systematists fooled by mimicry again!). Cast & Le Crom (2012) published the name *martinae* for the until then unnamed *H. melpomene* race. (image source: <https://cliniquevetodax.com/Heliconius/pages/melpomene%20martinae>).



FIGURE 74. Hybrid #41 (dorsal, ventral). Colombia: "Bogotá" (no collector or date indicated). Holotype of *Heliconius wernickei* Weymer, 1906. Housed in the NHMUK. Interpreted by Ackery & Smiles (1976) as a hybrid between *H. melpomene melpomene* and *H. cydno cydno*. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 backcross to *H. cydno*. The specimen exhibits all the typical pattern elements of *H. cydno cydno*, including yellow FW bands with hourglass mark, broad white HW bands reaching almost to the wing margin, and the HWV brown forceps pattern (somewhat truncated in this specimen, but not outside the range of normal variation for the race). The main "melpomene" element is the reddish brown band distal to the yellow band on the FW. The red FW band in *H. melpomene martinae* is located more proximally (overlapping the end of the discal cell), is orange-red to rosy-red, with a relatively sharp distal edge. Recall that lab-reared *H. melpomene* x *H. cydno* hybrids show a distally displaced red band as seen here (Fig. 57), but that the color is the same as the *H. melpomene* parent, not the reddish brown seen here and elsewhere (e. g., Hybrids #29, 30, 32).

Identity: 0.3

Authenticity: 0.2 (poor locality data)

Overall reliability: 0.06



FIGURE 75. Hybrid #42 (dorsal, ventral—note that the dorsal image was digitally altered to smooth damage to the forewing margins). Colombia: Caldas, Victoria, 2 Jan.(?) 1966, leg. E. Schmidt-Mumm (IAvH). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 backcross to *H. cydno* (see nomenclatural notes under #41). This specimen, also from the Magdalena Valley, is phenotypically very similar to Hybrid #41, except for the narrower HW band. The concern about Schmidt-Mumm labels indicated under Hybrid #14 applies here as well.

Identity: 0.3

Authenticity: 0.8

Overall reliability: 0.24



FIGURE 76. Hybrid #43 (dorsal, ventral). Colombia: Muzo, 400–800 m. 1907–1908, leg. Fassl. Holotype of *H. emilius* Weymer, 1912; Specimen housed in the NHMUK. Interpreted by Ackery & Smiles (1976) as a hybrid between *H. melpomene melpomene* and *H. cydno cydno*. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under #41). Anton H. H. Fassl was a collector/dealer who supplied butterflies and beetles to various European collectors. The specimen lacks the FW hourglass mark in the discal cell and the yellow/red band is shifted distally towards the wing tip. The red coloration is brighter than that of previous specimens. On the HWV, the posterior brown forceps mark is absent and the submarginal white band is partly suppressed. All of these features are similar to the lab-reared F1 shown in Fig. 56, suggesting that it is an F1.

Identity: 0.9

Authenticity: 0.9

Overall reliability: 0.81



FIGURE 77. Hybrid #44 (dorsal, ventral). Colombia: Boyacá, Otanche, 1986, leg. J. Urbina. From Neukirchen collection, now housed at FLMNH. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* ((Fig. 72) F1 (see nomenclatural notes under Hybrid #41). This specimen is quite similar to Hybrid #43, although the red band is composed of more brownish scales and the HWV submarginal band is very faint (but see F1 in Fig. 56). Presumably, F1 offspring of the same two parental races should be heterozygotes that exhibit a consistent pattern representing the dominant allele at each wing pattern locus. Thus, differences such as the breadth and faintness of the HW band as seen, for example, between this specimen and #43 are incompatible with both being F1s of the same two parental forms. The collector, José Urbina, is a Colombian lepidopterist whose specimens appear in the collections of Neukirchen, Schmidt-Mumm, Le Crom, as well as the commercial trade (e. g., <http://www.ksl-auction.com/auction.cgi?acc=disp&no=1482721588&t=1350171566>). This is one of eleven interspecific hybrid specimens in the Mallet *et al.* (2007) database ostensibly collected by Urbina (also #50, 53, 54, 57–63). It is notable that the collection dates on these specimens span a period of more than 20 years (1980–2001), with only two of them being collected in the same year. When a single, at least some-time commercial collector manages to capture multiple interspecific hybrid novelties, all from the same place, over two decades, and nobody else seems to have visited this remarkable locality to investigate its "hybrid zone," it provokes a degree of skepticism regarding the specimens' authenticity as wild-caught hybrids. Given the law of supply and demand, the value of the specimens from a reared brood would be greater if they were sold individually, rather than all put on the market at once. Also, selling them one at a time would increase the plausibility of the narrative that they were "wild caught."

Identity: 0.8

Authenticity: 0.1 (likely reared for the commercial trade)

Overall reliability: 0.08



FIGURE 78. Hybrid #45 (dorsal, ventral). Colombia (no further data) (NHMUK). Syntype of *H. rubellius* Grose-Smith & Kirby, 1892. Interpreted by Ackery & Smiles (1976) as a hybrid between *H. melpomene melpomene* and *H. cydno cydno*. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). The faintness and proximal shift of the HW submarginal band on the dorsal surface is unlike other putative F1 crosses of these two races (but see F1 in Fig. 56). There appears to be a shadow of a subcostal band on the HWV that is reminiscent of that seen in *H. cydno weymeri* Staudinger, 1896, from the Cauca Valley, where no form of *H. melpomene* occurs. Given the lack of specific locality data, it is difficult to interpret what this specimen is.

Identity: 0.3

Authenticity: 0.8

Overall reliability: 0.24



FIGURE 79. Hybrid #46 (dorsal, ventral). Colombia: "Santa Fé de Bogotá," 1907, leg. Donckler (NHMUK). There are a number of other Colombian butterflies in the NHMUK collected by Donckler and likely shipped to London from Bogotá. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). The faintness and proximal shift of the HW submarginal band on the dorsal surface is unlike other putative F1 crosses of these two races. Given the lack of specific locality data, it is difficult to interpret what this specimen is.

Identity: 0.4

Authenticity: 0.8

Overall reliability: 0.32



FIGURE 80. Hybrid #47 (dorsal, ventral). Colombia (no further data). From the Riffarth collection in the NHMUK (not "collected" by Riffarth in the sense of catching it in the forest). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). The faintness of the HW submarginal band on the dorsal surface is unlike other putative F1 crosses of these two races. Like Hybrid #45, there appears to be a shadow of a subcostal band on the HWV that is reminiscent of that seen in *H. cydno weymeri* Staudinger, 1896, from the Cauca Valley, where no form of *H. melpomene* occurs. Given the lack of specific locality data, it is difficult to interpret what this specimen is.

Identity: 0.3

Authenticity: 0.8

Overall reliability: 0.24



FIGURE 81. Hybrid #48 (dorsal, ventral). Colombia, Muzo, 400–800m. 1907–1908, leg. Fassl. (Same data as Hybrid #43). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Given the logic about F1 phenotypes discussed above (Hybrid #44), this specimen, #43 and #44 are very unlikely to all be F1 hybrid offspring of the same two races. Here, the HW submarginal band is completely absent on the dorsal surface and a shadow on the HWV. The shadow of the HWV subcostal band is again present. Neither of these is a feature of *H. cydno cydno*, casting doubt on the identity and/or locality of this specimen.

Identity: 0.4

Authenticity: 0.7

Overall reliability: 0.28



FIGURE 82. Hybrid #49 (dorsal, ventral). Colombia: "Santa Fé de Bogotá," from the Rothschild Bequest to the NHMUK (1939). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Specimen is very similar to #48, and additionally lacks plausible locality data.

Identity: 0.4

Authenticity: 0.5

Overall reliability: 0.2



FIGURE 83. Hybrid #50 (dorsal, ventral). Colombia: Boyacá, Otanche, 2 Jan. 1980, leg. J. Urbina. From Schmidt-Mumm collection (IAvH). Salazar (1993) suggested that Ernesto Schmidt-Mumm collected this specimen himself, but it seems he obtained it from José Urbina (see Hybrid #44). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Specimen is very similar to Hybrid #45, and is likely not an F1, given the clear expression of the HWV brown forceps.

Identity: 0.8

Authenticity: 0.1 (likely reared for the commercial trade)

Overall reliability: 0.08



FIGURE 84. Hybrid #51 (dorsal, ventral). Colombia: Caldas, Victoria, 24 June (?) 1960, Leg. E. Schmidt-Mumm. (IAvH). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Lack of a HW submarginal band but presence of complete HWV brown forceps suggests that this cannot be an F1 of the indicated races. This problem could be a result of the label issue mentioned above (Hybrid #14).

Identity: 0.6

Authenticity: 0.8

Overall reliability: 0.48



FIGURE 85. Hybrid #52 (dorsal, ventral). Colombia: Caldas, Río la Miel, 1.8 km N. Victoria, 28 Sept. 1969, leg. D. Brezing (NMS). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Specimen is quite similar to Hybrid #46.

Identity: 0.8

Authenticity: 1.0

Overall reliability: 0.8



FIGURE 86. Hybrid #53 (dorsal). Colombia: Boyacá, Otanche, 1990, Schmidt-Mumm collection (IAvH). Salazar (1993) suggested that Ernesto Schmidt-Mumm collected this specimen himself, but it seems he obtained it from José Urbina (see Hybrid #44). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Very similar to Hybrid #51. Even though the specimen is in rather poor condition, its provenance (from Urbina, like so many other hybrids between these two races) suggests that it, too, was reared.

Identity: 0.8

Authenticity: 0.1 (likely reared for the commercial trade)

Overall reliability: 0.08



FIGURE 87. Hybrid #54 (dorsal, ventral). Colombia: Boyacá, Otanche, 1986, leg. José Urbina (see Hybrid #44). Neukirchen collection (FLMNH). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Very similar to #46, and could be an F1 between the two races indicated.

Identity: 0.8

Authenticity: 0.1 (likely reared for the commercial trade)

Overall reliability: 0.08



FIGURE 88. Hybrid #55 (dorsal, ventral). Colombia: "Cundinamarca, Veraguas." Neustetter collection (NMW). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Locality is in Bogotá, which is probably from where the specimen was shipped to H. M. Neustetter (an Austrian entomologist and specimen dealer). The forewing of this specimen is superficially reminiscent of that of *H. heurippa* (Fig. 148), but the HW has *H. cydno* characters such as the ventral brown forceps (partially obscured by the labels due to careless photographic technique). Note that the diffuse submarginal HW band is shifted proximally relative to most of the other specimens in this group, suggesting the pattern of *H. cydno wanningeri* (Fig. 89). Given the poor locality data, the specimen is difficult to interpret.

Identity: 0.6

Authenticity: 0.3

Overall reliability: 0.18



FIGURE 89. *Heliconius cydno wanningeri* Neukirchen, 1991 (dorsal, ventral). COLOMBIA: Santander (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20waningeri.html>)



FIGURE 90. Hybrid #56 (dorsal, ventral). Colombia: Boyacá, Otanche, 2001, Le Crom Collection. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 backcross to *H. cydno* (see nomenclatural notes under Hybrid #41), due to the strongly expressed HW submarginal band. The brick-red distal forewing patch is the only "melpomene-like" character. The lack of detailed information about the circumstances under which the specimen was obtained (the supposed collector, J. Urbina, is followed by a question mark on the specimen's data label) and the fact that the Le Crom collection contains so many striking hybrids, suggests a commercial origin, and that the specimen may not have been collected in the wild.

Identity: 0.7

Authenticity: 0.1

Overall reliability: 0.07



FIGURE 91. Hybrid #57 (dorsal, ventral). Colombia: Boyacá, Otanche, 1999, leg. J. Urbina? (see Hybrid #44), Le Crom Collection. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 backcross to *H. cydno* (see nomenclatural notes under Hybrid #41). The brick-red distal forewing patch is the only "melpomene-like" character. The fact that the Le Crom collection contains so many striking "hybrids" of somewhat mysterious origin suggests that the specimen may not have been collected in the wild.

Identity: 0.7

Authenticity: 0.1

Overall reliability: 0.07



FIGURE 92. Hybrid #58 (dorsal, ventral). Colombia: Boyacá, Otanche, Oct. 1985, leg. José Urbina? (see Hybrid #44). Le Crom Collection. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Very similar to Hybrids #46 and #54, and could be an F1 between the two races indicated. However, as with the other Urbina specimens, the probability that the specimen was "wild caught" is low.

Identity: 0.8

Authenticity: 0.1 (likely reared)

Overall reliability: 0.08



FIGURE 93. Hybrid #59 (dorsal, ventral). Colombia: Boyacá, Otanche, Sept. 1986, leg. José Urbina? (see Hybrid #44). Le Crom Collection. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Very similar to Hybrids #46, #54, and #55, and could be an F1 between the two races indicated.

Identity: 0.8

Authenticity: 0.1 (likely reared)

Overall reliability: 0.08



FIGURE 94. Hybrid #60 (dorsal, ventral). Colombia: Boyacá, Otanche, April, 1988, leg. José Urbina? (see Hybrid #44). Le Crom Collection. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Very similar to Hybrids #46, #54, #55, and #59, and could be an F1 between the two races indicated.

Identity: 0.8

Authenticity: 0.1 (likely reared)

Overall reliability: 0.08



FIGURE 95. Hybrid #61 (dorsal, ventral). Colombia: Boyacá, Otanche, March, 1983, leg. José Urbina? (see Hybrid #44). Le Crom Collection. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Very similar to Hybrids #46, #54, #55, #59 and #60, and could be an F1 between the two races indicated.

Identity: 0.8

Authenticity: 0.1 (likely reared)

Overall reliability: 0.08



FIGURE 96. Hybrid #62 (dorsal, ventral). Colombia: Boyacá, Otanche, Sept. 1993, leg. José Urbina? (see Hybrid #44). Le Crom Collection. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Very similar to Hybrids #46, #54, #55, #59, #60, and #61, and could be an F1 between the two races indicated.

Identity: 0.8

Authenticity: 0.1 (likely reared)

Overall reliability: 0.08



FIGURE 97. Hybrid #63 (dorsal, ventral). Colombia: Boyacá, Otanche, Jan. 1991, leg. José Urbina? (see Hybrid #44). Le Crom Collection. Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "{euryas}" (Fig. 73) x *H. cydno cydno* (Fig. 72) F1 (see nomenclatural notes under Hybrid #41). Very similar to Hybrids #46, #54, #55, #59—#62, and could be an F1 between the two races indicated.

Identity: 0.8

Authenticity: 0.1 (likely reared)

Overall reliability: 0.08

Other Colombian putative *H. cydno* x *H. melpomene* hybrids from the Magdalena Valley



FIGURE 98. Hybrid #64 (dorsal, ventral). Colombia: Huila, San José Isnos, 6 July (?) 1990, leg. J. Le Crom (Le Crom collection). Interpreted by Mallet *et al.* (2007) as a *H. melpomene* "*euryas*" x *H. cydno cydno* F1 backcross to *H. cydno* (see nomenclatural notes under #41). The locality where the specimen was collected is in the range of *H. cydno lisethae* (Fig. 99), and the submarginal FW spots suggest that it belongs to that race and not *H. cydno cydno* (Fig. 72; it is surprising that Mallet *et al.* 2007 coauthor Neukirchen did not notice this error). All the characters of this specimen are *cydno*-like except for the distal brick-red band on the forewing. Note, again, that this color does not appear in any Colombian *H. melpomene*.

Identity: 0.8

Authenticity: 0.8

Overall reliability: 0.64



FIGURE 99. *H. cydno lisethae* Neukirchen, 1995 (dorsal, ventral). Colombia: Huila, San Agustín. (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20lisethae>)



FIGURE 100. Hybrid #65 (dorsal, ventral). "Nouve Granade" (no additional locality data). Holotype of *H. aventina* Oberthür, 1925 (NHMUK). Viewed by Ackery & Smiles (1976) as a *H. cydno hermogenes* x *H. melpomene melpomene* hybrid; viewed by Mallet *et al.* (2007) as a *H. melpomene* "*{euryas}*" (Fig. 73) x *H. cydno hermogenes* (Fig. 101) F1 (see nomenclatural notes under Hybrid #41). *H. cydno hermogenes* occurs in the upper Magdalena Valley, between the ranges of *H. cydno lisethae* (Fig. 99) to the south, and *H. cydno cydno* (Fig. 72) to the north. *H. cydno hermogenes* is the only *H. cydno* race with a double row of marginal/submarginal spots on the FW. This specimen has characters most consistent with that race, other than the brick-red patch distal to the discal cell on the forewing and the absent hourglass mark in the FW discal cell. Note also that the FW spots are elongated into streaks. Given the lack of locality data, this specimen could also possibly represent a hybrid with a red-banded form of *H. heurippa*.

Identity: 0.4

Authenticity: 0.4 (due to lack of locality data)

Overall reliability: 0.16



FIGURE 101. *H. cydno hermogenes* Hewitson [1858] (dorsal, ventral). Colombia: [Tolima], Rio Chili. (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20hermogenes>). Note that the infrasubspecific named form "*lutescens*" Kaye, 1916 has yellow, instead of white spots on the forewing.

Putative *H. melpomene* x *H. cydno* hybrids from Chocó, Colombia

Hybrid #66 (not illustrated—see plate 35, #4b in Holzinger & Holzinger, 1994. —That figure, quite similar to Hybrid #43, shows a rusty-red distal forewing band on an otherwise rather typical—looking *H. cydno* phenotype). "W. Colombia" leg. E. Krüger. Holotype of *H. cydno chioneus* f. "*eugenius*" Niepelt, 1928. NMW(?). Interpreted (presumably on the basis of the locality data) by Mallet *et al.* (2007) as *H. cydno chioneus*? (Fig. 60) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*. The available information on this specimen renders it impossible to interpret.

Identity: 0.0

Authenticity: 0.2

Overall reliability: 0.0



FIGURE 102. *H. melpomene vulcanus* Butler, 1865 (dorsal, ventral). Colombia: [Valle del Cauca], Río Dagua. This is one of the most striking forms of *H. melpomene*, with a blueish iridescence on the dorsal surface and a fine fringe of white scales on the wing margins. Also note that the transverse yellow HW band is only expressed on the ventral surface. (image source: <https://cliniquevetodax.com/Heliconius/pages/melpomene%20vulcanus.html>).



FIGURE 103. Hybrid #67 (dorsal). Colombia (W. Colombia), leg. E. Krüger (MZPW). Interpreted (presumably on the basis of the locality data) by Mallet *et al.* as *H. cydno chioneus* (Fig. 60) x *H. melpomene vulcanus* (Fig. 102) F1. The HW submarginal band does not reach the margin, which does not reflect the typical pattern in *H. cydno chioneus*. The FW band in *H. melpomene vulcanus* is compact, well-defined and carmine-red, not the brick-red of the red patch here. The vague locality data on this specimen (label in image is illegible) render it difficult to interpret. It may be a hybrid between some alternative races, or possibly an atavistic mutant.

Identity: 0.2

Authenticity: 0.5

Overall reliability: 0.1



FIGURE 104. Hybrid #68 (dorsal, ventral). Colombia: Chocó, Río San Juan, Palestrina. 1988. leg. C. Farrell. Neukirchen Collection (FLMNH). Interpreted by Mallet *et al.* (2007) as a *H. cydno zeline* (Fig. 105) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*, based on the large white forewing band and completely expressed brown forceps on the HWV. The apparent source of this specimen, as well #69-#71 and #85 and #86, was Christopher Farrell, a commercial butterfly dealer who resided in Bogotá, Colombia in the 1980's (Johnson & Matusik, 1986; see also <http://insectnet.proboards.com/thread/441>) (not Clive Farrell, owner of large butterfly houses in the U.S. and the U.K. with many captive-reared *Heliconius*). Given the commercial source, and that other specimens in the Neukirchen Collection are also of dubious authenticity, the parsimonious explanation is that this specimen was reared for the trade.

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09



FIGURE 105. *H. cydno zeline* Butler, 1869 (dorsal, ventral). Colombia: Cali, Río Dagua [the race occurs on the Pacific slope in Valle del Cauca and Chocó, not in the Cauca Valley where Cali is situated]. (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20zeline.html>).



FIGURE 106. Hybrid #69 (dorsal, ventral). Colombia: Chocó, Río San Juan, Palestrina. 1988. leg. C. Farrell. Neukirchen Collection (FLMNH). Interpreted by Mallet *et al.* (2007) as a *H. cydno zeline* (Fig. 105) x *H. melpomene vulcanus* (Fig. 102) F1, based on the larger red forewing band and yellowish tint to the anterior band of the brown forceps on the HWV (*H. melpomene vulcanus* has a yellow stripe on the HWV). As with Hybrid #68, this specimen likely was reared for the commercial trade.

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09



FIGURE 107. Hybrid #70 (dorsal, ventral). Colombia: Chocó, Río San Juan, Palestrina. 1988. leg. C. Farrell. Neukirchen Collection (FLMNH). Interpreted by Mallet *et al.* (2007) as a *H. cydno zeline* (Fig. 105) x *H. melpomene vulcanus* (Fig. 102) F1. Specimen is quite similar to Hybrid #69, and interpreted to have the same provenance.

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09



FIGURE 108. Hybrid #71 (dorsal, ventral). Colombia: Chocó, Río San Juan, Palestrina. 1988. leg. C. Farrell. Neukirchen Collection (FLMNH). Interpreted by Mallet *et al.* (2007) as a *H. cydno zelinde* (Fig. 105) x *H. melpomene vulcanus* (Fig. 102) F1, based on the larger red forewing band and partial suppression of the brown forceps on the HWV. Also likely reared for commerce.

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09

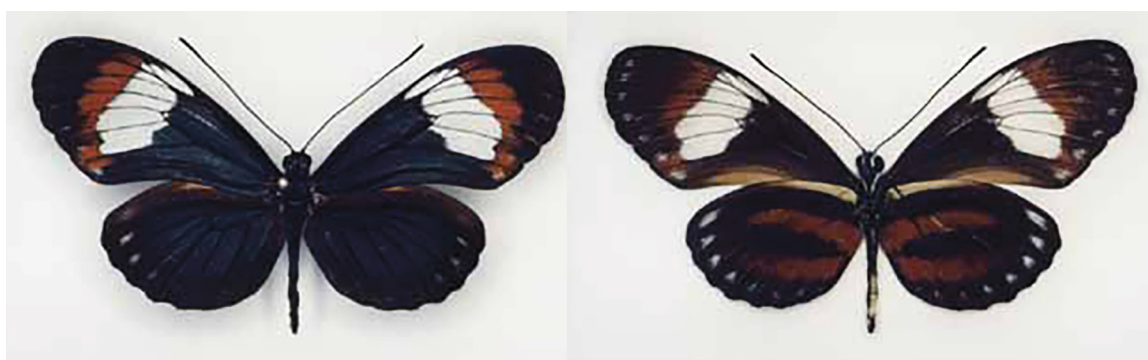


FIGURE 109. Hybrid #85 (dorsal, ventral). Colombia: Valle, Río Calima, near Río Bravo, 1200m. 1988. leg. C. Farrell. Neukirchen Collection (FLMNH). Interpreted by Mallet *et al.* (2007) as a *H. cydno zelinde* (Fig. 105) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*. Other than the slightly wider white FW band and the different locality data, this specimen appears to fit rather well into this series of material "collected" by dealer Farrell.

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09



FIGURE 110. Hybrid #86 (dorsal, ventral). Colombia: Valle, Río Calima, near Río Bravo, 1200m. 1988. leg. C. Farrell. Neukirchen Collection (FLMNH). Interpreted by Mallet *et al.* (2007) as a *H. cydno zelinde* (Fig. 105) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*. Very similar to Hybrid #69, but with different locality data. This specimen also appears to fit rather well into the series of material "collected" by dealer Farrell.

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09

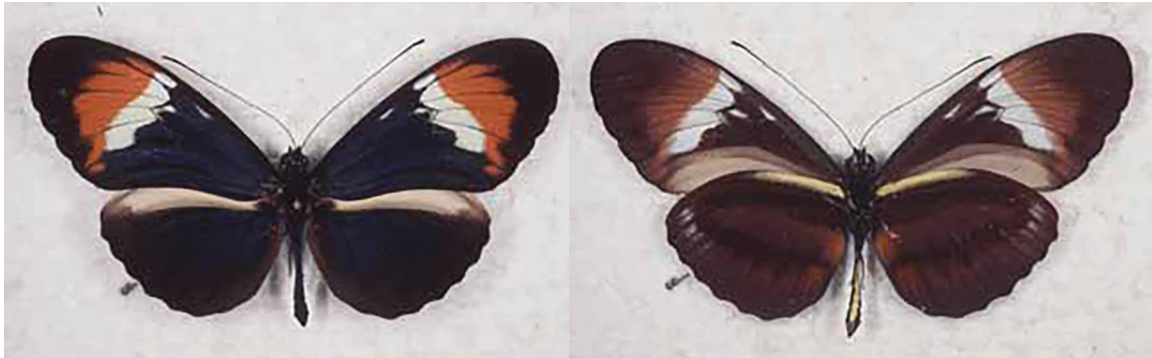


FIGURE 111. Hybrid #72 (dorsal, ventral). Colombia: Valle, Cali, 1973. Leg. L. Denhez? Mast de Maeght coll. (RBINS—James Mast de Maeght donated his large butterfly collection to the Royal Belgian Institute of Natural Sciences in 2015). Interpreted by Mallet *et al.* (2007) as a *H. cydno zelinde* (Fig. 105) x *H. melpomene vulcanus* (Fig. 102) F1, based on the larger red forewing band and partial suppression of the brown forceps on the HWV. León Denhez (and his son Leoncito?) were commercial collectors based in Cali, whose atypical *Heliconius* material appears not only in Mast de Maeght's collection, but also in the Holzinger and Neukirchen collections. It is likely that the locality data on the label are the source of the material from the dealer, rather than the place where the specimen was collected. This is supported by the high degree of similarity between this specimen and Hybrid #71, leading to Mallet *et al.*'s interpretation that the two represent crosses of the same races—the endemic race of *H. cydno* in the vicinity of Cali is *H. cydno cydnides* (Fig. 112), and there is no sympatric race of *H. melpomene* that occurs there. Once again, in light of the commercial origin of the specimen and the abundance of "hybrids" from this source in the collections of European amateurs, the provenance of the specimen is dubious.

Identity: 0.6 (poor locality data)

Authenticity: 0.1

Overall reliability: 0.06



FIGURE 112. *H. cydno cydnides* Staudinger, 1885 (dorsal, ventral). Colombia: "Valle del Cauca, Río Dagua" [probably incorrect locality data, as this race occurs in the Cauca Valley, not on the Pacific slope]. (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20cydnides>)



FIGURE 113. Hybrid #73 (dorsal, ventral). Colombia: Valle, Buenaventura, Isla Punta Soldado, 30 March(?) 2000. Efraín Henao collection (Universidad Nacional de Colombia, Bogotá). Interpreted by Mallet *et al.* (2007) as a *H. cydno zelinde* (Fig. 112) x *H. melpomene vulcanus* (Fig. 102) F1. The specimen is quite similar to Hybrid #72, except with a more ragged outer margin to the FW red band, and a lack of submarginal white spots on the HWV. This specimen was collected by a butterfly biologist, and looks like it actually spent some time flying around before that event.

Identity: 0.9

Authenticity: 1.0

Overall reliability: 0.9



FIGURE 114. Hybrid #74 (dorsal, ventral). Colombia: Valle, Río Calima, Estación Agrícola del Bajo Calima, 1979, leg. A. Jaramillo (ICNB). Interpreted by Mallet *et al.* (2007) as a *H. cydno zelinde* (Fig. 112) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. melpomene*. The specimen appears to have a shadow yellow stripe on the dorsal HW (apparently absent on the VHW), which is not a characteristic of *H. melpomene vulcanus*. It does not look like any of the other Chocó hybrids, and could be an aberrant *H. melpomene*.

Identity: 0.6

Authenticity: 1.0

Overall reliability: 0.6



FIGURE 115. Hybrid #75 (dorsal, ventral). Colombia: Valle, Cali, 1969. Leg. L. Denhez? Mast de Maeght coll. (RBINS). See provenance notes under Hybrid #72. Interpreted by Mallet *et al.* (2007) as *H. cydno weymeri* f. "*weymeri*" (Fig. 116) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*, based on the narrow yellow bar on the hindwing. The "hybrid" features are very subtle, and given the likely commercial origin and poor locality data of this specimen, it cannot be regarded as evidentially reliable.
 Identity: 0.6 (poor locality data)
 Authenticity: 0.1
 Overall reliability: 0.06



FIGURE 116. *H. cydno weymeri* Staudinger 1897 ("typical" form, dorsal, ventral). Colombia: Río Cauca valley. This race is polymorphic (see Fig. 118).



FIGURE 117. *H. cydno weymeri* f. "*gustavi*" Staudinger, 1897 (dorsal, ventral). Colombia [no further locality data]. The name *gustavi* is an intrasubspecific quadrinomial and not available under the ICZN Code (ICZN, 1999). Some "*gustavi*" individuals have pure black forewings. This specimen is atypical, with white spots on the FW and a partial brown forceps on the VHW. It may be an intraspecific hybrid backcross to another *H. cydno* form (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20weymeri>).



FIGURE 118. Hybrid #76 (dorsal, ventral). Colombia: Valle, Río Dagua, 1987. Leg. L. Denhez/Gerstner. Neukirchen collection (FLMNH). Interpreted by Mallet *et al.* (2007) to be a *H. cydno weymeri* f. "gustavi" (Fig. 117) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*, due to the faint red FW bands. A commercially-obtained specimen from Denhez (see Hybrid #73) via Gerstner (see Hybrid #23). There is no reason to believe that this specimen was collected in the wild.

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09



FIGURE 119. Hybrid #77 (dorsal, ventral). Colombia: Valle, Río Dagua, (no date). Leg. L. Denhez/Gerstner. Neukirchen collection (FLMNH). Interpreted by Mallet *et al.* (2007) to be a *H. cydno weymeri* f. "gustavi" (Fig. 117) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*, due to the faint red FW bands. As for Hybrid #76, there is no reason to believe that this specimen was collected in the wild.

Identity: 0.9

Authenticity: 0.1

Overall reliability: 0.09



FIGURE 120. Hybrid #78 (dorsal, ventral). Colombia: Valle, Río Dagua, 1969. Leg. L. Denhez. NMW (Holzinger collection?). Interpreted by Mallet *et al.* (2007) as a *H. cydno weymeri* f. "weymeri" (Fig. 116) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*, based on the presence of the yellow bar on the HWV only. It is not immediately clear why this specimen could not be an intraspecific hybrid of *H. cydno weymeri* (Fig. 116) x *H. cydno cydnides* (Fig. 112), which meet in a well-studied hybrid zone in Valle del Cauca (cf. Linares 1997). Holzinger & Holzinger (1968) described several infrasubspecific forms of *H. cydno* that they obtained from Denhez via Gerstner (including forms "denhezi" and "gerstneri"), now deemed to be hybrids between these two *H. cydno* races (cf. Lamas & Jiggins 2017). Regardless of its identity, the commercial provenance diminishes the specimen's plausibility as a wild-caught hybrid.

Identity: 0.5

Authenticity: 0.1

Overall reliability: 0.05



FIGURE 121. Hybrid #79 (dorsal, ventral). Colombia: Valle, Rio Dagua, 1969. Leg. L. Denhez? Mast de Maeght collection (RBINS). Interpreted by Mallet *et al.* (2007) as a *H. cydno weymeri* f. "weymeri" (Fig. 116) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*, based on the partial expression of the yellow bar on the dorsal and ventral HW. See Hybrid #78 for explanation.

Identity: 0.5

Authenticity: 0.1

Overall reliability: 0.05



FIGURE 122. Hybrid #80 (dorsal, ventral). Colombia: Valle, Rio Dagua, 1967. Leg. L. Denhez? Mast de Maeght collection (RBINS). Interpreted by Mallet *et al.* (2007) as a *H. cydno weymeri* f. "weymeri" (Fig. 116) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*, based on the relatively narrow yellow bar on the HWV. See Hybrid #78 for explanation.

Identity: 0.5

Authenticity: 0.1

Overall reliability: 0.05



◀ **FIGURE 123.** Hybrid #81 (dorsal, ventral). Colombia: Valle, Rio Dagua, ~1970. Leg. Gerstner. Mast de Maeght collection (RBINS). Interpreted by Mallet *et al.* (2007) as a *H. cydno zelinde* (Fig. 105) x *H. melpomene vulcanus* (Fig. 102) F1 or perhaps backcross to *H. melpomene*, based on the broad brown forceps on HWV. See Hybrids #69 and #73. As stated above, Hermann Gerstner was a commercial dealer, and middle man for sellers of novelties. Given its provenance and perfect condition, this specimen is not plausible as a wild-caught hybrid.

Identity: 0.8

Authenticity: 0.1

Overall reliability: 0.08



FIGURE 124. Hybrid #82 (dorsal, ventral). Colombia: Valle, Rio Dagua, 1968. Leg. L. Denhez? Mast de Maeght collection (RBINS). Interpreted by Mallet *et al.* (2007) as a *H. cydno weymeri* f. "weymeri" (Fig. 116) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*, based on the partial expression of the yellow bar on the dorsal and ventral HW. See Hybrid #79. Commercial origin as described above.

Identity: 0.5

Authenticity: 0.1

Overall reliability: 0.05



FIGURE 125. Hybrid #83 (dorsal, ventral). Colombia: Valle, Rio Dagua, 1966. Leg. L. Denhez? Mast de Maeght collection (RBINS). Interpreted by Mallet *et al.* (2007) as a *H. cydno weymeri* f. "weymeri" (Fig. 116) x *H. melpomene vulcanus* (Fig. 102) F1 backcross to *H. cydno*, based on the partial expression of the yellow bar on the dorsal and ventral HW. See Hybrid #79. Commercial origin as described above.

Identity: 0.5

Authenticity: 0.1

Overall reliability: 0.05



FIGURE 126. Hybrid #84 (dorsal, ventral). Colombia: Valle, Rio Dagua, 1966. Leg. L. Denhez. Mast de Maeght collection (RBINS). Paratype of *H. cydno gerstneri* f. *pseudoweymeri* H. & R. Holzinger, 1968 (an unavailable infrasubspecific quadrinomial). Interpreted by Mallet et al. (2007) as a *H. cydno weymeri* f. “*weymeri*” (Fig. 116) x *H. melpomene vulcanus* (Fig. 102) backcross to *H. cydno*, as but see #78. Furthermore, likely commercial origin as described above.

Identity: 0.5

Authenticity: 0.1

Overall reliability: 0.05

Putative *H. cydno cordula* x *H. melpomene melpomene* hybrids from Venezuela

A series of specimens from Táchira in western Venezuela exhibit what appear to be intermediate *H. cydno* x *H. melpomene* phenotypes. Apparent hybrids have been collected in this area since at least 1980, so it seems that there is a stable hybrid zone of some sort that has persisted for at least 35 years. Many of the more recent hybrid specimens were genotyped with AFLP markers by Mávarez *et al.* (2006), who said, “the hybrid individuals cannot be distinguished from other individuals of *H. cydno*, indicating that multiple generations of backcrossing must have occurred.” This is an odd result—particularly given that even the putative F1 backcross to *H. melpomene* (Mávarez Hybrid #34, Fig. 135) has an essentially pure *H. cydno* genotype at the AFLP loci. Brower (2011) predicted that these specimens might represent not interspecific *H. cydno* x *H. melpomene* hybrids, but hybrids between *H. cydno cordula* and an unrecognized red-banded member of the *H. cydno* clade. In light of the genetic evidence, and given the number of recently-discovered *H. cydno* cognates on the east side of the Andes, this hypothesis seems at least as parsimonious as an interspecific cross. Therefore, all of the Táchira specimens (Mávarez Hybrids #28-#34 and Hybrids #87-#96 from the Mallet *et al.* (2007) database are interpreted as interracial, not interspecific hybrids, and given an identity score of zero. This is clearly an important area for further investigation to fill in our understanding of the distribution and phenotypic variation of the *H. cydno*—*H. heurippa* clade.



FIGURE 127. Mávarez #1 (dorsal, ventral). Venezuela: Táchira, San Cristobal, Jardín Botánico de Táchira, 1060m. Oct. 2003. Leg. J. Mávarez. One of 60 individual specimens of "pure" *H. cydno cordula* Neustetter, 1913, sampled by Mávarez from this site. Bodies of these specimens were removed for DNA analysis. (image source for this and the following "Mávarez" specimens <https://www.biomedcentral.com/content/supplementary/1471-2148-7-28-s1/mavarez/cristobaltab.html>).



FIGURE 128. Mávarez #35 (dorsal, ventral). Venezuela: Táchira, San Cristobal, Jardín Botánico de Táchira, 1060m. Oct. 2003. Leg. J. Mávarez. One of 36 individual specimens of "pure" *H. melpomene melpomene* sampled from this site.



FIGURE 129. Mávarez Hybrid #28 (dorsal, ventral). Venezuela: Táchira, San Cristobal, Jardín Botánico de Táchira, 1060m. Oct. 2003. Leg. J. Mávarez. Interpreted by Mallet *et al.* (2007) as *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno* (presumably due to the missing hourglass element in the FW discal cell).
Identity: 0.0
Authenticity: 1.0
Overall reliability: 0.0



FIGURE 130. Mávarez Hybrid #29 (dorsal, ventral). Venezuela: Táchira, San Cristobal, Jardín Botánico de Táchira, 1060m. Oct. 2003. Leg. J. Mávarez. Interpreted by Mallet *et al.* (2007) as *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno* (presumably due to the missing hourglass element in the FW discal cell).
Identity: 0.0
Authenticity: 1.0
Overall reliability: 0.0



FIGURE 131. Mávarez Hybrid #30 (dorsal, ventral). Venezuela: Táchira, San Cristobal, Jardín Botánico de Táchira, 1060m. Oct. 2003. Leg. J. Mávarez. Interpreted by Mallet *et al.* (2007) as *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno* (presumably due to the brick-red band distal to the yellow band on the FW).
Identity: 0.0
Authenticity: 1.0
Overall reliability: 0.0



FIGURE 132. Mávarez Hybrid #31 (dorsal, ventral). Venezuela: Táchira, San Cristobal, Jardín Botánico de Táchira, 1060m. Oct. 2003. Leg. J. Mávarez. Interpreted by Mallet *et al.* (2007) as *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno* (presumably due to the brick-red band distal to the yellow band on the FW).
Identity: 0.0
Authenticity: 1.0
Overall reliability: 0.0



FIGURE 133. Mávarez Hybrid #32 (dorsal, ventral). Venezuela: Táchira, San Cristobal, Jardín Botánico de Táchira, 1060m. Oct. 2003. Leg. J. Mávarez. Interpreted by Mallet *et al.* (2007) as *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno* (presumably due to the brick-red band distal to the yellow band on the FW). Identity: 0.0
Authenticity: 1.0
Overall reliability: 0.0



FIGURE 134. Mávarez Hybrid #33 (dorsal, ventral). Venezuela: Táchira, San Cristobal, Jardín Botánico de Táchira, 1060m. Oct. 2003. Leg. J. Mávarez. Interpreted by Mallet *et al.* (2007) as *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno* (presumably due to the missing hourglass element in the FW discal cell). Identity: 0.0
Authenticity: 1.0
Overall reliability: 0.0



FIGURE 135. Mávarez Hybrid #34 (dorsal, ventral). Venezuela: Táchira, San Cristobal, Jardín Botánico de Táchira, 1060m. Oct. 2003. Leg. J. Mávarez. Interpreted by Mallet *et al.* (2007) as *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. melpomene* (due to the reduced brown forceps mark on the HWV.).
 Identity: 0.0
 Authenticity: 1.0
 Overall reliability: 0.0



FIGURE 136. Hybrid # 87 (dorsal, ventral). Venezuela: Táchira, Parque Nacional Paramillo, 1140m. Leg. M. Linares. Interpreted by Mallet *et al.* (2007) as a *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno*. The ragged condition of the inscribed wings and absence of a body suggest that this female was kept in an insectary before being ground up for DNA analysis.
 Identity: 0.0
 Authenticity: 1.0
 Overall reliability: 0.0



FIGURE 137. Hybrid # 88 (dorsal, ventral). Venezuela: Táchira, Parque Nacional Paramillo, 1140m. Leg. M. Linares. Interpreted by Mallet *et al.* (2007) as a *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno*.
 Identity: 0.0
 Authenticity: 1.0
 Overall reliability: 0.0



FIGURE 138. Hybrid # 89 (dorsal, ventral). Venezuela: Táchira, Parque Nacional Paramillo, 1140m. Leg. M. Linares. Interpreted by Mallet *et al.* (2007) as a *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno*, presumably due to the missing hourglass mark in the FW discal cell.

Identity: 0.0

Authenticity: 1.0

Overall reliability: 0.0



FIGURE 139. Hybrid # 90 (dorsal, ventral). Venezuela: Táchira, Parque Nacional Paramillo, 1140m. Leg. M. Linares. Interpreted by Mallet *et al.* (2007) as a *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno*, presumably due to the missing hourglass mark in the FW discal cell.

Identity: 0.0

Authenticity: 1.0

Overall reliability: 0.0



FIGURE 140. Hybrid # 91 (dorsal, ventral). Venezuela: Táchira, Parque Nacional Paramillo, 1140m. Leg. M. Linares. Interpreted by Mallet *et al.* (2007) as a *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno*, presumably due to the missing hourglass mark in the FW discal cell.

Identity: 0.0

Authenticity: 1.0

Overall reliability: 0.0



FIGURE 141. Hybrid #92 (dorsal, ventral). Venezuela: Táchira, Río Negro, 11-13 Dec. 1980. Leg. José A. Clavijo (UCVM). Interpreted by Brown & Fernández (1985) and by Mallet *et al.* (2007) as a *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1.

Identity: 0.0

Authenticity: 1.0

Overall reliability: 0.0



FIGURE 142. Hybrid #93 (dorsal). Venezuela: Táchira(?), ~1980. This specimen is probably in the Romero family collection, Maracay. Interpreted by Mallet *et al.* (2007) as a *H. cydno cordula* (Fig. 127) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno*. It bears a striking superficial resemblance to *H. heurippa* (Fig. 148).

Identity: 0.0

Authenticity: 0.7

Overall reliability: 0.0



◀
FIGURE 143. Hybrid #94 (dorsal). Venezuela: Táchira(?), ~1980. This specimen is probably in the Romero family collection, Maracay. Interpreted by Mallet *et al.* (2007) as a *H. cydno gadouae* (Fig. 144) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno*. *H. cydno gadouae* has a white apical band and sometimes also a row of submarginal dots on the FW and a subapical white spot on the HW. Given the absence of white apical markings on the FW, this is probably another *H. cydno* (Fig. 127) hybrid.

Identity: 0.0

Authenticity: 0.7

Overall reliability: 0.0



FIGURE 144. *H. cydno gadouae* Brown & Fernández, 1985 (dorsal, ventral). Venezuela: Táchira, San Juan de Colon, 850m. (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%20gadouae>).

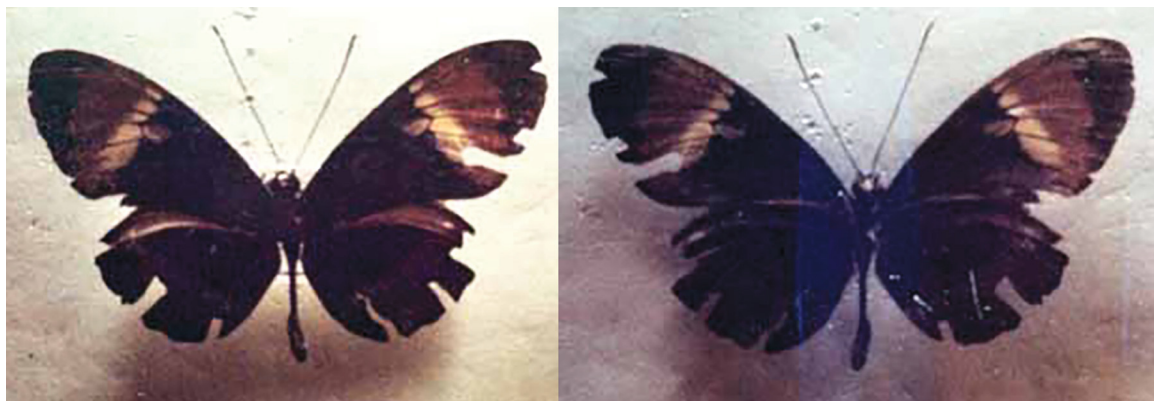


FIGURE 145. Hybrid #95 (dorsal, ventral). Venezuela: Barinas, Above Barinitas, 900 m, (no date) In the Mattei family collection. Interpreted by Brown & Fernández (1985) and by Mallet *et al.* (2007) as a *H. cydno barinasensis* (Fig. 146) x *H. melpomene melpomene* (Fig. 128) F1. These photos are underexposed. In Brown & Fernández (1985, Fig. 177), there is clearly a partial hourglass mark in the FW discal cell and a shadowy submarginal white band on the dorsal and ventral hindwing. Nevertheless, the brick-red distal forewing band is not found in the local *H. melpomene*.

Identity: 0.0

Authenticity: 0.7

Overall reliability: 0.0



FIGURE 146. *H. cydno barinasensis* Masters, 1973 (dorsal, ventral). Venezuela: [Cojedes], Las Minas. (image source: <https://cliniquevetodax.com/Heliconius/pages/cydno%barinasensis>)



FIGURE 147. Hybrid #96 (dorsal, ventral). Venezuela: possibly Barinas, Above Barinitas, 900 m, (no date) In the Mattei family collection. Interpreted by Mallet *et al.* (2007) as a *H. cydno barinasensis* (Fig. 146) x *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. cydno*. These photos are underexposed. In Brown & Fernández (1985), a similar specimen (from Táchira, La Fundación, 1400m, 16 Feb. 1976, leg. KS Brown. Jr.) is illustrated (their #169), which is interpreted as a *H. cydno cordula* (Fig. 127) x *H. cydno barinasensis* (Fig. 146) interracial hybrid. Neither of these interpretations seems correct. *H. cydno barinasensis* has a broad white submarginal HW band, and this would surely be visible in a backcross if it is evident in an F1 (see Hybrid #95, Fig. 145, above). Likewise, both *H. cydno cordula* and *H. cydno barinasensis* have a broad FW band, with at least a partial hourglass mark in the discal cell. Given its questionable locality data and its similarity to Brown's specimen from La Fundación, this specimen can be interpreted the same way as Hybrids #89-#91.

Identity: 0.0

Authenticity: 0.4 (misleading locality data)

Overall reliability: 0.0

Putative hybrid between *H. heurippa* and *H. melpomene melpomene*



FIGURE 148. *Heliconius heurippa* Hewitson, [1854] (dorsal, ventral). Colombia: Meta, Villavicencio. Coll. M. Demaio. On both surfaces of the forewing, note the large yellow hourglass mark in the discal cell and the narrow strip of black scales between the yellow and brick-red bands. On the HWV, note the absence of brown forceps marks characteristic of most *H. cydno* forms, presence of red basal spots, and marginal white dots (dorsal as well). (image source: <https://cliniquevetodax.com/Heliconius/pages/heurippa.html>).

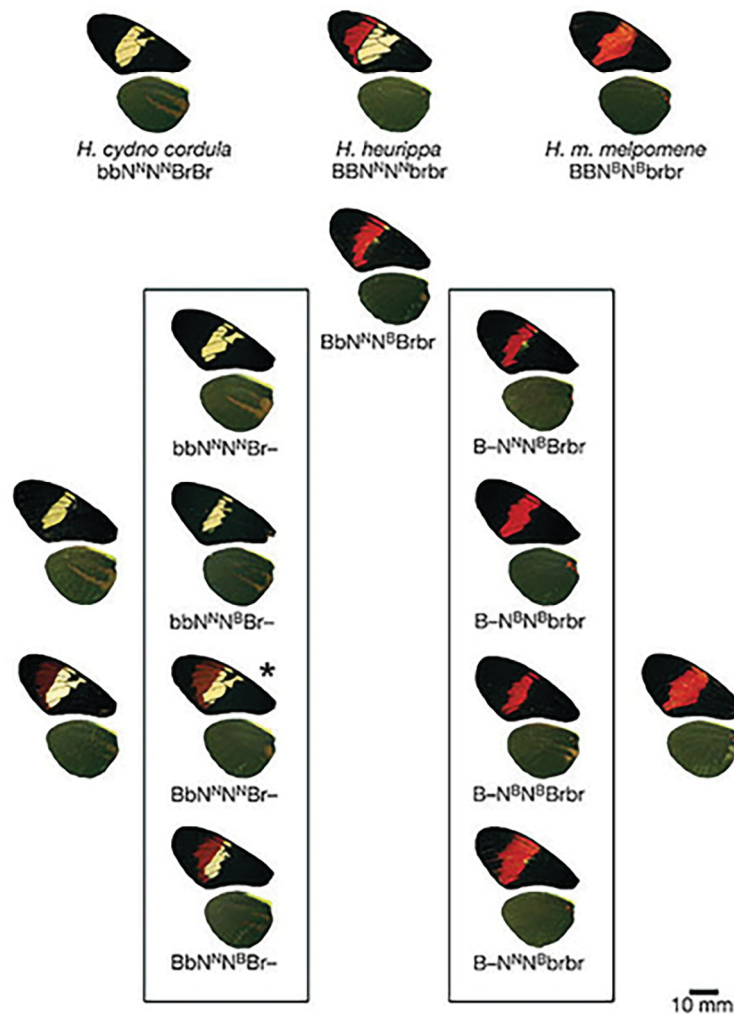


FIGURE 149. Experimental crosses by Mávarez *et al.* (2006): *H. cydno cordula*, *H. heurippa* and *H. melpomene melpomene* parental forms, (top row) *H. cydno cordula* x *H. melpomene melpomene* hybrid F1 (2nd row) and backcross phenotypes (in boxes). Individuals to left and right of boxes are Mávarez hybrid specimens #28 (Fig. 129), 29 (Fig. 130) and 34 (Fig. 135). (Image source: <http://evolucionarios.blogalia.com/historias/40884>). All wings shown FWD and HWV. The fact that the specimen at the bottom of the left box has a different phenotype from the F1, even though their indicated genotypes are the same, shows that there must be additional genes involved in expression of the two patterns than the three described in the figure. There are also evident epistatic interactions involving the yellow forewing band, the HWV forceps mark and the color and distal displacement of the red band: for example, the expression of the HW forceps mark is complete in Brbr heterozygotes in the *H. cydno* backcross, but is only partly expressed in the Brbr heterozygote in the *H. melpomene* backcross.

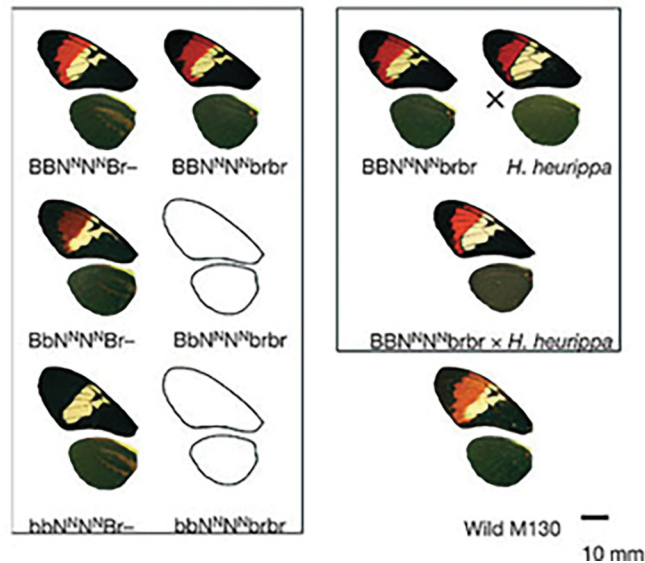


FIGURE 150. Experimental crosses by Mávarez *et al.* (2006; Image source: <http://evolucionarios.blogalia.com/historias/40884>). *H. cydno cordula* × *H. melpomene melpomene* F3 phenotypes from the F2 phenotype with asterisk in Fig. 149 (left). Homozygous hybrid phenotype crossed to *H. heurippa* and F1 offspring (right) The individual below the right box is a wild specimen from San Cristobal, similar to (or the same individual as) #88 (Fig. 137). Note that the heterozygous condition of the B allele changes the color of the FW red band from rosy-red to brick-red.



FIGURE 151. Hybrid #97 (dorsal, ventral). Colombia: Cundinamarca, Chirijara (sic), 1991, leg. D. Acosta (according to Mallet *et al.* 2007) or D. Silva (according to Salazar 1993). Schmidt-Mumm collection (IAvH). Interpreted by Mallet *et al.* (2007) as a *H. heurippa* (Fig. 148) × *H. melpomene melpomene* (Fig. 128) F1 backcross to *H. heurippa*. As may be seen in Figure 149, this phenotype does not appear in crosses of the putative "parental" species of *H. heurippa*, nor in a cross of those hybrids back to *H. heurippa* (Fig. 150). Note also that the red band is more proximal, almost reaching the end of the FW discal cell, and that this specimen lacks the fine line of black scales between the yellow and red forewing band seen in *H. heurippa*. Phenotypes such as this one appear in crosses between "postman" patterned *H. melpomene* with a red FW band and "dennis-ray" patterned *H. melpomene* in French Guiana and elsewhere, and at this locality, it is not implausible that this specimen is a *H. melpomene melpomene* × *H. melpomene malleti* (Fig. 14) F1 backcross to *H. melpomene melpomene*.

Identity: 0.0

Authenticity: 0.9

Overall reliability: 0.0

Putative hybrids between *H. cydno galanthus* and *H. pachinus* from Costa Rica



FIGURE 152. *Heliconius pachinus*_Salvin, 1871(dorsal, ventral). Costa Rica: Cerro Chirripo. Image source: <https://cliniquevetodax.com/Heliconius/pages/pachinus.html>

Heliconius cydno galanthus (Fig. 54) is a widespread Central American race of that occurs from southern Mexico to the western end of Panama, where it intergrades into *H. cydno chioneus* (Fig. 60). *H. pachinus* is endemic to the Pacific slope in southeastern Costa Rica and western Panama, where other *H. cydno* forms are absent. Kronforst *et al.* (2006a) were able to hybridize the two and produce fertile offspring in captivity. Their illustrations show that F1 offspring are black and white, generally similar to *H. cydno galanthus*, but with a narrower FW band that does not extend into the discal cell, and no HW markings (regrettably, characters on the ventral surface were not illustrated or discussed).

The status of *H. pachinus* as a distinct species from *H. cydno* has been subject to alternative interpretations. Brower (1996a, 2013), Mallet *et al.* (1998), Gilbert (2003) and Lamas (2004) viewed it as a subspecies or geographical race of *H. cydno*, and Kronforst *et al.* (2007) called *H. pachinus* "a lineage within the cydno clade." To lend support to their argument for "interspecific hybridization", Mallet *et al.* (2007) viewed *H. pachinus* and *H. cydno* as "parapatric species pairs," and the Lamas and Jiggins (2017) checklist indicates *H. pachinus* as a distinct species. DeVries (1987) said, "in Villa Colon both species fly together and occasionally hybridize," and Gilbert (2003) suggested the existence of a hybrid zone between these forms in the Costa Rican Meseta Central: "it is now clear that a hybrid zone has been present but not perceived, since many hybrid individuals, due to the nature of wing pattern genetics in this group, display rather novel phenotypes ...". Nevertheless, only three hybrid specimens, all of which are minor variants of the normal *H. cydno galanthus* phenotype, are documented in the database.



FIGURE 153. Hybrid # 98 (ventral). Costa Rica. The specimen was collected on the slopes of Turrialba volcano (Volcán Irazu?), on the Atlantic slope of Costa Rica, (USNM type no. 16782) and bears Schaus' label "*H. galanthus* var. *subrufescens*". However, the published description (Schaus, 1913) categorizes the specimen as an aberration: thus, the name is infrasubspecific and unavailable (ICZN Art. 45.6.2). Gilbert (2003, plate 14.5) illustrated the specimen, incorrectly stating that "this Costa Rican specimen of *H. cydno* was described as a new species by Schaus (1913)" and observed that it is similar to one of the F2 phenotypes arising from a *H. cydno* x *H. pachinus* cross (see Hybrid #99). Mallet *et al.* (2007) erroneously reported that the specimen is housed in Vienna (it is in the USNM). Interpreted by Mallet *et al.* (2007) to be a backcross between a *H. cydno galanthus* x *H. pachinus* F1 and *H. cydno galanthus*, based on the large brown oval on the HWV, which is not typical of *H. cydno galanthus* (although there appears to be substantial individual variation in the expression of the brown patterns of the HWV of that subspecies). The specimen exhibits no features indicative of *H. pachinus*.

Identity: 0.2

Authenticity 1.0

Overall reliability: 0.2



FIGURE 154. Hybrid #99 (ventral). Mallet *et al.* (2007) misleadingly implied that this is a wild hybrid specimen from Rio Sarapiquí, Costa Rica, and count it as such in their Table 1. The figure legends in the database (and Gilbert 2003, plate 14.5, where the image is reproduced) indicate to the contrary, that the specimen is a lab -reared *H. cydno galanthus* x *H. pachinus* backcross of indeterminate pedigree from the "synthetic hybrid zone" in Larry Gilbert's greenhouse at UT Austin.

Identity: 1.0

Authenticity 0.0 (not a wild-caught hybrid)

Overall reliability: 0.0



FIGURE 155. Hybrid #100 (dorsal, ventral). Costa Rica: Heredia, La Selva Biological Station, 17 July 2002, leg. K. Kronforst. Mallet *et al.* (2007) interpreted this specimen as another hybrid backcross between a *H. pachinus* (Fig. 152) x *H. cydno galanthus* (Fig. 54) F1 and *H. cydno galanthus*. The atypical features are the reduced anterior brown "forceps" in the HW, and the reduction of the white hourglass-shaped pattern element in the apex of the FW discal cell.

Identity: 0.2

Authenticity: 1.0

Overall reliability: 0.2

Hybrids # 98 and 100 (#99 is not a wild-caught hybrid) have no characters typical of *H. pachinus*, but could represent backcrosses, given that most of the *H. cydno* alleles are dominant. Unfortunately, the backcross phenotypes are so similar to the wing pattern of the somewhat variable phenotype of *H. cydno galanthus* (Fig. 54) that it is difficult to draw firm conclusions about their hybrid origins. Given the alleged existence of a hybrid zone in an area long-frequented by *Heliconius* biologists, and anecdotal reports of additional hybrids collected in the field (Kronforst *et al.* 2006b), it is surprising that there are not more specimens formally documented. Finally, as discussed above, the specific distinctness of *H. pachinus* from *H. cydno* is debatable.

Hybrids between *H. erato* and *H. himera* from western Ecuador and Peru



FIGURE 156. *H. erato cyrbia* Godart, 1819 (dorsal, ventral). Ecuador: Pichincha, Région de Lita, Chuchuví. Found on the Pacific slope of Ecuador, where it is the co-mimic of *H. melpomene cythera* (Fig. 61). (image source: <https://cliniquevetodax.com/Heliconius/pages/erato%20cyrbia.html>)



FIGURE 157. *H. himera* Hewitson, 1867 (dorsal, ventral). Peru: Amazonas, Bagua, 500–1000m. (image source: <https://cliniquevetodax.com/Heliconius/pages/himera.html>).

For most of the 20th century, *H. himera* was viewed as a race of *H. erato* (Eltringham 1916; Brown 1979), and from a phylogenetic perspective, *H. himera* is nested among various races of a paraphyletic *H. erato* (Brower 1994b; Hines *et al.* 2011; Supple *et al.* 2015; Van Belleghem *et al.* 2017). These two taxa are parapatric in southern Ecuador, where *H. erato cyrbia* prefers wetter, lower forest, and *H. himera* occurs in higher, drier *Acacia* scrub, however they abut in a narrow hybrid zone (Jiggins *et al.* 1996). Descimon & Mast de Maeght (1984) suggested a "semispecies" relationship between the two, due to a deficit of observed hybrid specimens from numbers expected if the parental forms were mating at random. Based on this observation, Mallet (1993, p.245) opined, "it is more sensible to regard *H. himera* as a good species." Mallet (1995) proposed the "genealogical cluster concept" of species to accommodate taxa such as *H. himera*, which while still hybridizing at appreciable frequency with its sister taxon appears to have reached a tipping point at which homogenizing gene flow does not occur. We will return to Mallet's species concept in the discussion.

Mallet *et al.* (2007) listed a series of 52 hybrid specimens between *H. erato cyrbia* and *H. himera* (three exemplars of which are shown below: Figs. 158–160). The genetics of wing pattern inheritance were experimentally worked out by Jiggins *et al.* (1996), and there is no doubt that these specimens are legitimate hybrids. Thus, hybrids #101–152 are given the following collective scores:

Identity: 1.0

Authenticity: 1.0

Overall reliability: 1.0



FIGURE 158. Hybrid #111 (dorsal, ventral). *H. erato cyrbia* (Fig. 156) x *H. himera* (Fig. 157) F1 (dorsal, ventral). Ecuador: El Oro, Guayquichuma site 4, 1993 (Neukirchen collection, FLMNH). The yellow forewing bands are replaced with red, but otherwise the specimen looks like *H. himera*.



FIGURE 159. Hybrid #110 (dorsal, ventral). *H. erato cyrbia* (Fig. 156) x *H. himera* (Fig. 157) backcross to *H. himera*. Ecuador: El Oro, Guayquichuma site 4, 1993. leg. S. Attal (Neukirchen collection, FLMNH). There is a faint pinkish edge on the distal margin of the yellow forewing band.



FIGURE 160. Hybrid #117(dorsal, ventral). *H. erato cyrbia* (Fig. 156) x *H. himera* (Fig. 157) backcross to *H. erato*. Ecuador: El Oro, Guayquichuma site 4, 1993. leg. S. Attal (Neukirchen collection, FLMNH). Both *H. himera*'s red HW band and the yellow HWV stripe of *H. erato cyrbia* are expressed in this individual.



FIGURE 161. *Heliconius erato favorinus* Hopffer, 1874 (dorsal, ventral). Peru: Huanuco, Tingo Maria. (image source: <https://cliniquevetodax.com/Heliconius/pages/erato%20favorinus.html>)



FIGURE 162. Hybrid #153 (dorsal). Peru: San Martín, Rodriguez de Mendoza, 1500m. Nov. 1984, leg. F. König, König collection (NMW). Austrian Fritz König (d. 2102) lived and collected in Peru from 1954-1980's(?), and his collection was donated to Naturhistorisches Museum, Wien after his death. König (1986) reported this specimen as an intraspecific hybrid (viewing *H. himera* as a race of *H. erato*). Mallet *et al.* (2007) interpret it as an *H. erato favorinus* (Fig. 161) x *H. himera* (Fig. 157) F1. Given the locality and what is known about inheritance of the various wing pattern elements in these hybrids (Jiggins *et al.* 1996), this interpretation seems plausible.

Identity: 1.0

Authenticity: 1.0

Overall reliability: 1.0



◀ **FIGURE 163.** Hybrid #154 (dorsal, ventral). Peru: San Martín, Rodríguez de Mendoza, 1994, leg. M. Bueche. Neukirchen coll. (FLMNH). Interpreted by Mallet *et al.* (2007) as an *H. erato favorinus* (Fig. 161) x *H. himera* (Fig. 157) backcross to *H. erato*—presumably based on the locality data. The distal margin of the FW red band is not like either of the putative parental forms, and the truncation of the yellow HW band is also not evident in other putative *H. erato* x *H. himera* hybrids. Further, this specimen is very similar to the holotype of *Heliconius amatus* Staudinger, 1897 (see http://www.butterfliesofamerica.com/L/ih/heliconius0490_i.htm), which is considered to be a *H. erato phyllis* (Fabricius, 1775) x *H. erato venustus* Salvin, 1871 backcross to *H. erato phyllis*. As noted for the specimen illustrated in Fig. 42, Martin Bueche runs a butterfly house in France. It is very probable that that the locality data are false, and it may well have been reared in captivity.

Identity: 0.5

Authenticity: 0.2

Overall reliability: 0.1

Hybrid #155 (not illustrated in Mallet *et al.* 2007). Peru: San Martín, Rodríguez de Mendoza-Omia km 11, 1986, leg. J. Mallet (Mallet collection). Interpreted by Mallet *et al.* (2007) as *H. himera* (fig. 157) x *H. erato favorinus* (fig. 161). This specimen cannot be independently evaluated from the evidence presented. *Habeas corpus!*

Identity: 0.

Authenticity: 1.0

Overall reliability: 0.0



FIGURE 164. Hybrid #156 (dorsal). Peru: San Martín, Rodríguez de Mendoza-Omia km 11, ~1986. König collection (NMW). Interpreted by Mallet *et al.* (2007) as *H. himera* (Fig. 157) x *H. erato favorinus* (Fig. 161) backcross to *H. erato*. The locality data of this specimen are the same as Hybrid #155. König (1986) does not mention this specimen, but it is not as dramatic a hybrid as Hybrid #153. The shape of the FW red band is more consistent with those of the putative parental forms than is that of Hybrid #154.

Identity: 0.9

Authenticity: 0.8

Overall reliability: 0.72



◀ **FIGURE 165.** Hybrid #15 (dorsal). 7. Peru: Amazonas: Aramango, <1990. König coll. (NMW). Interpreted by Mallet *et al.* (2007) as a *H. erato lativitta* (Fig. 166) x *H. himera* (fig. 157) F1. The dennis and ray pattern of this specimen, combined with the position and shape of the yellow FW band and the red transverse basal band on the HW represent a tidy combination of features of the putative parental forms. Mallet (1993) reported finding no hybrids in the putative zone of contact between *H. himera* and *H. erato lativitta* (in his collections, the two populations were geographically separated by approximately 10 km).

Identity: 1.0

Authenticity: 0.9

Overall reliability: 0.9



FIGURE 166. *H. erato lativitta* Butler, 1877 (dorsal, ventral). Peru: Loreto, Iquitos, Río Momon, Oct.–Dec. 1986. (image source: <https://cliniquevetodax.com/Heliconius/pages/erato%20lativitta.html>)

Putative *H. erato* x *H. charithonia* hybrid



FIGURE 167. Hybrid #158 (dorsal, ventral). Mexico: Oaxaca, Sierra Juarez, Chiltepec [San Juan Quiotepec?], 1970, leg. A. Díaz Francés (UNAM). Originally hypothesized to be an aberrant *H. erato* by de la Maza (1991), Mallet *et al.* (2007) interpreted this specimen as an *H. erato petiverana* (Fig. 168) *H. charithonia vasquezae* (fig. 169) F1 or backcross to *H. erato*. Based on wing shape (particularly the acute apex of the HW), the specimen is clearly not an *H. erato*, and there is little else to suggest that it has any genetic contribution from that species. It appears to be an aberrant *H. charithonia*. Note also the absence of basal red spots on the HWV, which are present in both putative parents—perhaps indicative of developmental anomalies. A recently posted image (Fig. 170) shows a *H. sara* with a genetically modified (knockout) WntA gene, whose phenotype exhibits the loss of a large area of black pigment on the forewing. This suggests that the enlarged yellow forewing patch (or absence of black pigment) of the above hybrid could be the result of a mutation.

Identity: 0.1

Authenticity: 1.0

Overall reliability: 0.1



FIGURE 168. *H. erato petiverana* Doubleday, 1847 (dorsal, ventral). Mexico: Veracruz, Nanciyaga. (image source: <https://cliniquevetodax.com/Heliconius/pages/erato%20petiverana.html>)



FIGURE 169. *H. charithonia vasquezae* Comstock & Brown, 1950 (dorsal, ventral). Guatemala: Monte Rico, Santa Rosa. (image source: <https://cliniquevetodax.com/Heliconius/pages/charithonia%20vazquezae.html>)



FIGURE 170. *H. sara sara* (Fabricius, 1793) wild-type phenotype (dorsal, ventral, above) and genetically modified WntA knockout mutant (dorsal, ventral, below). (image source: <http://www.pnas.org/content/suppl/2017/08/29/1708149114.DCSupplemental>).

Putative *H. charithonia* x *H. peruvianus* hybrid

Hybrid #159 (not illustrated in Mallet *et al.* (2007). Ecuador: Pichincha, Río Toachi, 1700m. 1996 leg. C. Jiggins (Jiggins collection). This butterfly, documented by Jiggins & Davies (1998), has an *H. charithonia* phenotype (cf.

Fig. 169), but a distribution of allozyme alleles that suggested to them an F1 hybrid between *H. charithonia* and *H. peruvianus* (Fig. 171). Mallet *et al.* (2007) interpreted it as backcross to *H. charithonia*, likely due to its homozygous condition of malic enzyme for an allele that is nearly absent from *H. peruvianus*. There are no fixed differences among the alleles examined by Jiggins & Davies (1998) between these two species, so it is possible that it is *H. charithonia*. (Also note that prior to Jiggins and Davies' study, *H. peruvianus* was viewed as a race of *H. charithonia*).

Identity: 0.9

Authenticity: 1.0

Overall reliability: 0.9



FIGURE 171. *H. peruvianus* C. Felder & R. Felder, 1859 (dorsal). Ecuador: "Esmeraldas, Lita, Chuchuví" (locality data erroneous—K. Willmott pers. comm.). (image source: <https://cliniquevetodax.com/Heliconius/pages/peruvianus.html>). This taxon, elevated from subspecific status by Jiggins & Davies (1998), is a dry-forest segregate from western Ecuador like *H. himera*.

Putative *H. hecalesia* Hewitson, 1854 hybrids



FIGURE 172. Hybrid #160 (dorsal, ventral). Mexico: Oaxaca, Valle Nacional, 1200 m. 1987 leg. T. Porion. Neukirchen coll. (FLMNH). Interpreted by Mallet *et al.* (2007) as an *H. hortense* (Fig. 173) x *H. hecalesia octavia* (Fig. 174) F1 hybrid. That identity of the specimen seems entirely plausible. However, the "collector," Thierry Porion, is a French insect dealer. As with many of the Neukirchen specimens, this one's authenticity as a "wild-caught hybrid" is cast into doubt by its commercial origin.

Identity: 1.0

Authenticity: 0.1

Overall reliability: 0.1



FIGURE 173. *H. hortense* Guérin, 1844 (dorsal, ventral; two different specimens). Mexico: [Veracruz], Las Tuxtlas (dorsal); Mexico: Chiapas (ventral.) (image source: <https://cliniquevetodax.com/Heliconius/pages/hortense.html>)



FIGURE 174. *H. hecalesia octavia* Bates, 1866 (dorsal, ventral). Mexico: Oaxac, Metates, 1400m, leg. Y. Lever. (image source: <https://cliniquevetodax.com/Heliconius/pages/hecalesia%20octavia.html>)



FIGURE 175. Hybrid #161 (dorsal, ventral). Costa Rica: Cartago, Jicotea, Turrialba, 1100m, 1995, leg. G. Vega, A. Valerio (MNCR). Interpreted by Mallet *et al.* (2007) to be a *H. clysonymus montanus* (Fig. 177) x *H. hecalesia formosus* (Fig. 176) F1. Although superficially similar to Hybrid #160 (Fig. 172), this specimen differs notably in the absence of white submarginal spots on the HW, and in the shape of the tawny HWD region, which is intermediate between that of *H. hecalesia octavia* (Fig. 174) and *H. hecalesia formosus*. The suffusion of pale scales in the subcostal area of the HWV is suggestive of that seen in *H. clysonymus*, but also of the HWV of *H. hecalesia octavia*. Since the specimen exhibits no features unequivocally derived from *H. clysonymus*, it could be a melanic aberration of *H. hecalesia*.

Identity: 0.5

Authenticity: 1.0

Overall reliability: 0.5



FIGURE 176. *H. hecalesia formosus* Bates, 1866 (dorsal, ventral). Panama (indicated as the same specimen, but the antennae and separation of the left pair of wings suggest otherwise). (image source: <https://cliniquevetodax.com/Heliconius/pages/hecalesia%20formosus.html>)



FIGURE 177. *H. clysonymus montanus* Salvin, 1871 (dorsal, ventral). Costa Rica: Chirripo. (image source: <https://cliniquevetodax.com/Heliconius/pages/clysonymus%20montana>).



FIGURE 178. And finally, Hybrid specimen #06-921 (dorsal, ventral). Not included in Mallet *et al.* (2007). Peru: San Martín, Rumiyaçu, near Moyobamba 06°05'23"S 76°58'09"W, 2006 (?), no collector indicated (MUSM). Image source: https://www.researchgate.net/publication/6036804_Genetic_analysis_of_a_wild-caught_hybrid_between_non-sister_Heliconius_butterfly_species/figures). This rather rubbed specimen was sequenced for mtDNA COI-COII and for several nuclear genes (invected, Mpi, Tpi, Tektin, Rpl5), which exhibited double bands in the chromatograms suggestive of a heterozygote condition. Dasmahapatra *et al.* (2007) interpreted these data to suggest that the specimen is an F1 heterozygote cross between *H. melpomene amaryllis* (Fig. 180) and *H. ethilla aerotome* (Fig. 179). The specimen's main *H. melpomene*-like morphological feature is a yellow transverse HWV band (a feature also found in a number of *H. ethilla* races). Otherwise, it looks mostly silvaniform, with reduced yellow and black markings on the FW, and a tawny postdiscal FW patch that Dasmahapatra *et al.* (2007) considered to represent the influence of *H. melpomene amaryllis*' red FW band. The basal red spot in HWV cell CU₂ characteristic of *H. ethilla* is not evident in the image, but it appears that the published figure has been rather clumsily modified to increase contrast and color saturation.



FIGURE 179. *H. ethilla aerotome* C. Felder & R. Felder 1862 (dorsal, ventral). Peru: San Martín, Juanjui. (image source: https://cliniquevetodax.com/Heliconius/pages/ethilla_aerotome.html). Note the tawny shading of the distal FW, and the yellowish tint of the transverse band on the HWV.



FIGURE 180. *H. melpomene amaryllis* C. Felder & R. Felder, 1862 (dorsal, ventral). Peru: San Martín, Satipo. (image source: <https://cliniquevetodax.com/Heliconius/pages/melpomene%20amaryllis.html>).

Although Genbank accession numbers were not reported in Dasmahapatra *et al.* (2007), most (but not all) of the sequences referred to in the paper are available in Genbank. Close examination of sequences from the "hybrid" and other *Heliconius* revealed some interesting facts. As reported, 06-921's 2119 bp mtDNA sequence (Genbank accession code AM709828) is virtually identical to that of *H. ethilla aerotome* 02-975 (AM709826), which strongly suggests that the mother of the specimen was an *H. ethilla*. The nuclear genes, with two alleles each, are more complicated. Teasing apart a chromatogram with heterozygous sites into two separate alleles is not an easy feat, but other than some description of "deconvolution" of sequences of variable length, Dasmahapatra *et al.* (2007) did not describe how they determined the sequences of alternate alleles, other than by comparing the heterozygous sites to the sequences of the two putative parental species. Needless to say, calling the bases so that they match one or the other parental sequence is hardly an independent corroboration of the allelic similarity of the "hybrid" to the parents. Indeed, several of these genes are known to exhibit dramatic heterozygosity of intron sequence and length within "pure" (i. e., not hybrid) individuals (Brower 2011), yet Dasmahapatra *et al.* (2007) used single sequences of *H. ethilla* and *H. melpomene* in their Neighbor-Joining analyses, apparently assuming that every other specimen except 06-921 was homozygous.

The two 06-921 Mpi "alleles" (AM709819, AM709820) were short (315 and 313 bp, respectively), and differed from one another only by a 2 base-pair indel. The former was identical to an Mpi sequence from *H. ethilla aerotome* 02-975 (AM709815.1), while the latter was identical to an Mpi sequence from *H. melpomene amaryllis* JM1917_A (AY332454.1) and from several other *H. melpomene* races. However, some *H. ethilla* Mpi sequences are more similar to *H. melpomene* sequences than they are to one another, and some Mpi sequences included in Dasmahapatra *et al.* (2007) fig. 2 are not present in GenBank. These problems cast doubt upon the value of these sequences as evidence for interspecific hybridization (cf. Brower 2011).

The two 06-921 invected sequences (AM709837 and AM709838), aligned below, were only 52 and 53 bp long, respectively:

```
CTTTTGTATCTTTTTTGTGTTT-ATTCAAATTACAAAGTTTGTAATACATACAT
ATTTTGTATCTTTTTTGTGTTTATTCAAATTATTAAGTTTGTAAGGCTCTTA
```

Most *Heliconius* invected sequences in Genbank are over 400 bp long, and Dasmahapatra *et al.* offered no explanation why these sequences are so truncated. Using Genbank's BLAST query (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>), the former is a perfect match to *H. ethilla aerotome* 02-3 sequence (AM709835, also only 52 bases long), while the latter is identical to a number of *H. melpomene* and *H. heurippa* sequences. However, when taken in a broader context (e. g., Brower 2011), neither available alleles for *H. melpomene* nor for silvaniform taxa form coherent groups for this gene. In any event, these tiny sequences do not provide much evidence for any pattern at all. Note also that the last 9 bases of these two sequences are not parsimoniously viewed as homologous sites when aligned with longer invected sequences from other *Heliconius*.

The specimen's two Tpi sequences, AM709812 (563 bp) and AM709813 (411 bp) differ from one another primarily by the presence or absence of several long indels. The longer sequence is identical to three *H. ethilla* sequences, while the shorter one is similar to *H. melpomene* sequences. As with Mpi, this gene region is known to exhibit individual heterozygosity in these indel regions (Brower 2011), and it is certainly not a safe assumption to use a single allele from local *H. ethilla* and *H. melpomene* races to authoritatively assign the affinities of alternate alleles from the "hybrid."

There is only one Tektin sequence in Genbank for 06-921 (AM709690), and Dasmahapatra *et al.* (2007) apparently sorted ambiguous chromatogram peaks from this sequence to match either an *H. melpomene* or an *H. ethilla* sequence. As noted above, such a procedure begs the question of the specimen's identity, and does not constitute evidence. The fifth nuclear gene, Rpl5, was uninformative by Dasmahapatra *et al.*'s admission, due to non-monophyly of alleles of *H. ethilla* and *H. melpomene* with respect to one another.

To sum up, Dasmahapatra *et al.*'s presentation of the molecular evidence endeavored to show that 06-921 is a *H. ethilla* x *H. melpomene* F1. However, the only marker that is not compromised by potentially unrealistic simplifying assumptions is the mtDNA, which only tells us about one parent. The molecular evidence thus leaves room for doubt about the plausibility of this specimen's hybrid origin.

Identity: 0.75

Authenticity: 0.9 (vague details of when and by whom the specimen was collected).

Overall reliability: 0.68

Discussion

The reliability score presented for each specimen above represents an effort to evaluate its fractional bona fides on a continuous scale, given consideration of its phenotype (or genotype), its provenance, and its history as a specimen in collections. In Table 1, Mallet *et al.*'s (2007) numbers of hybrids per species (including additional specimens discussed above that were not included in the original database) are compared against these scores at two different reliability cutoff levels. A relaxed level views any specimen with a score of less than 0.5 as likely not an interspecific hybrid, and any specimen with a score of 0.5 or greater as a potential interspecific hybrid. A more stringent reliability cutoff of .75 eliminates a few more "hybrid" specimens. Both of these sets of numbers are visually represented in Fig. 181. As noted in the introduction, these scores are subjective, but so, of course, were Mallet *et al.*'s (2007) determinations.

What the current results show is that, other than hybrids between *H. erato cyrbia* and the recently-elevated, parapatric *H. himera*, interspecific hybridization is rare, and always or almost always (depending on the reliability cutoff) between closely-related members of recently-differentiated clades. Most hypothesized silvaniform x *H. melpomene* hybrids have been reinterpreted as intra-silvaniform hybrids, and many of the *H. cydno* x *H. melpomene* crosses have been documented as almost certainly the result of captive rearing for the commercial specimen trade. With this reconsideration of the evidence, support for the hypothesis of "the species boundary as a continuum" of the Mallet *et al.* (2007) title largely disappears, and is replaced by a rather precipitous drop in records of hybridization between more inclusive clades (e. g. *cydno-melpomene* vs. silvaniforms—see Fig. 181), as well as among sympatric "biological" species.

Why do the numbers of hypothesized hybrids differ so much?

There are three main reasons why a specimen viewed by Mallet *et al.* (2007) as an interspecific hybrid may be viewed otherwise here. First, the hybrid may be morphologically ambiguous, so that the characters that suggest hybrid origin can be alternatively interpreted as intraspecific variation, aberration, etc. Such specimens received low "identity" scores above. Second, the specimen may be a hybrid, but not between the taxa suggested by Mallet *et al.* (2007). Hybrids of this type received high identity scores (if deemed to be interspecific), but an alternative hypothesis of parentage is proposed. Third is the problem of the chain of custody of the specimen from wherever it happened to live, to the collection where it currently resides. That sort of specimen may receive a high identity

score (e. g., it actually is a *H. cydno*—*H. melpomene* hybrid), but have its overall reliability eroded by questions about whether it was actually "collected in the wild."

TABLE 1. Numbers of wild interspecific hybridization events in *Heliconius*, as hypothesized by Mallet *et al.* (2007) and the current work (50% and 75% reliability thresholds presented). Uncorrected % pairwise sequence divergence from Mallet *et al.* (2007) supplement 3. Ages of divergence (millions of years ago) interpolated from the time-calibrated phylogenetic tree of Kozak *et al.* (2015).

Species 1	Species 2	% divergence	Age of divergence	Number of putative interspecific hybrids ¹			
				Mallet <i>et al.</i> (2007)	50%	75%	sum of scores ²
<i>H. numata</i>	<i>H. melpomene</i>	5.77	~4 mya	3	0	0	0.18
<i>H. numata</i>	<i>H. elevatus</i>	4.41	~3 mya	0	2	1	1.485
<i>H. hecale</i>	<i>H. melpomene</i>	4.39	~4 mya	2	0	0	0
<i>H. hecale</i>	<i>H. elevatus</i>	1.67	~2.5 mya	4	2	1	1.875
<i>H. pardalinus</i>	<i>H. elevatus</i>	(not reported)	~2 mya	2(?)*	1	1	0.81
<i>H. ethilla</i>	<i>H. melpomene</i>	5.34	~4 mya	5*	1	0	1.595
<i>H. ethilla</i>	<i>H. numata</i>	4.52	~2.5 mya	2	1	0	0.81
<i>H. ethilla</i>	<i>H. besckei</i>	3.56	~2.5 mya	6	3	3	3.15
<i>H. cydno</i>	<i>H. melpomene</i>	3.15	~2 mya	75*	7	4	10.84
<i>H. heurippa</i>	<i>H. melpomene</i>	3.17	~2 mya	1	0	0	0
<i>H. cydno</i>	<i>H. pachinus</i>	1.37	~1.5 mya	3	0	0	0.4
<i>H. erato</i>	<i>H. himera</i>	3.2	~2 mya	56	56	56	53.72
<i>H. erato</i>	<i>H. charithonia</i>	7.58	~4 mya	1	0	0	0.1
<i>H. peruvianus</i>	<i>H. charithonia</i>	3.76	~2.5 mya	1	1	1	0.9
<i>H. hecalesia</i>	<i>H. hortense</i>	6.77	~5mya	1	0	0	0
<i>H. hecalesia</i>	<i>H. clysonymus</i>	7.22	~5 mya	1	1	0	0.5
Total				163	75	67	76.465

* additional hybrids not mentioned in Mallet *et al.* (2007) that are discussed in the text above, such as the San Cristobal "*H. cydno* x *H. melpomene*" specimens are included in these totals.

¹ Some of the current values are higher than Mallet *et al.*'s numbers due to reinterpretation of identity of putative parental species.

² Values are the sum of "overall reliability" scores for all putative hybrids for the given species pair.

In the first category, the distal "reddish" forewing bands viewed as a genetic contribution from *H. melpomene* to *H. cydno* and a variety of silvaniform species have been taken as prima facie evidence of hybridization by Ackery & Smiles (1976), Brown (1976) and Mallet *et al.* (2007), among others. However, red wing pattern elements are symplesiomorphic for the *H. cydno*—*H. melpomene* clade (as for the entire genus *Heliconius*; Brower, 2011). Thus, the genetic "toolbox" of all these species, now identified as the optix gene and surrounding cis enhancer/suppressor binding sites (Reed *et al.*, 2011), already contains the raw materials to produce red wing pattern elements. In some instances, a mutation that suppresses the expression of melanic scales in a given wing region could result in the atavistic expression of underlying pattern elements, as seen in the yellow forewings of the artificial knockout *H. sara* (Fig. 170).

A similar introgression argument formed the basis of the "homoploid hybrid speciation" explanation (Mávarez *et al.* 2006) for the origin of *H. heurippa* (Fig. 148), which has a distal red forewing band but otherwise exhibits a generally *H. cydno*-like genetic constitution. However, it is now agreed (Arias *et al.* 2014; 2017; Jiggins 2017) that *H. heurippa* is phylogenetically nested among the taxa formerly classified as *H. timareta* Hewiston, 1867 (*H. timareta* and its subspecies/races should all be considered subspecies or geographical races of *H. heurippa*, which is has taxonomic priority as the species name). Several other forms of *H. heurippa* s. l. (*H. heurippa tristero* Brower, 1996b; *H. heurippa thelxinoe* Lamas & Mérot, 2013, not to mention *H. melpomene melpomene*-like "hybrids" from San Cristóbal, Venezuela see Fig. 135) also exhibit red forewing bands, and the parsimonious optimization of the character is that it is a plesiomorphic state for the *melpomene*-*cydno* clade. Thus, an alternative hypothesis is that red forewing bands in *H. cydno* forms may be explained, potentially more parsimoniously, by atavistic reversal rather than by repeated introgression from *H. melpomene*.

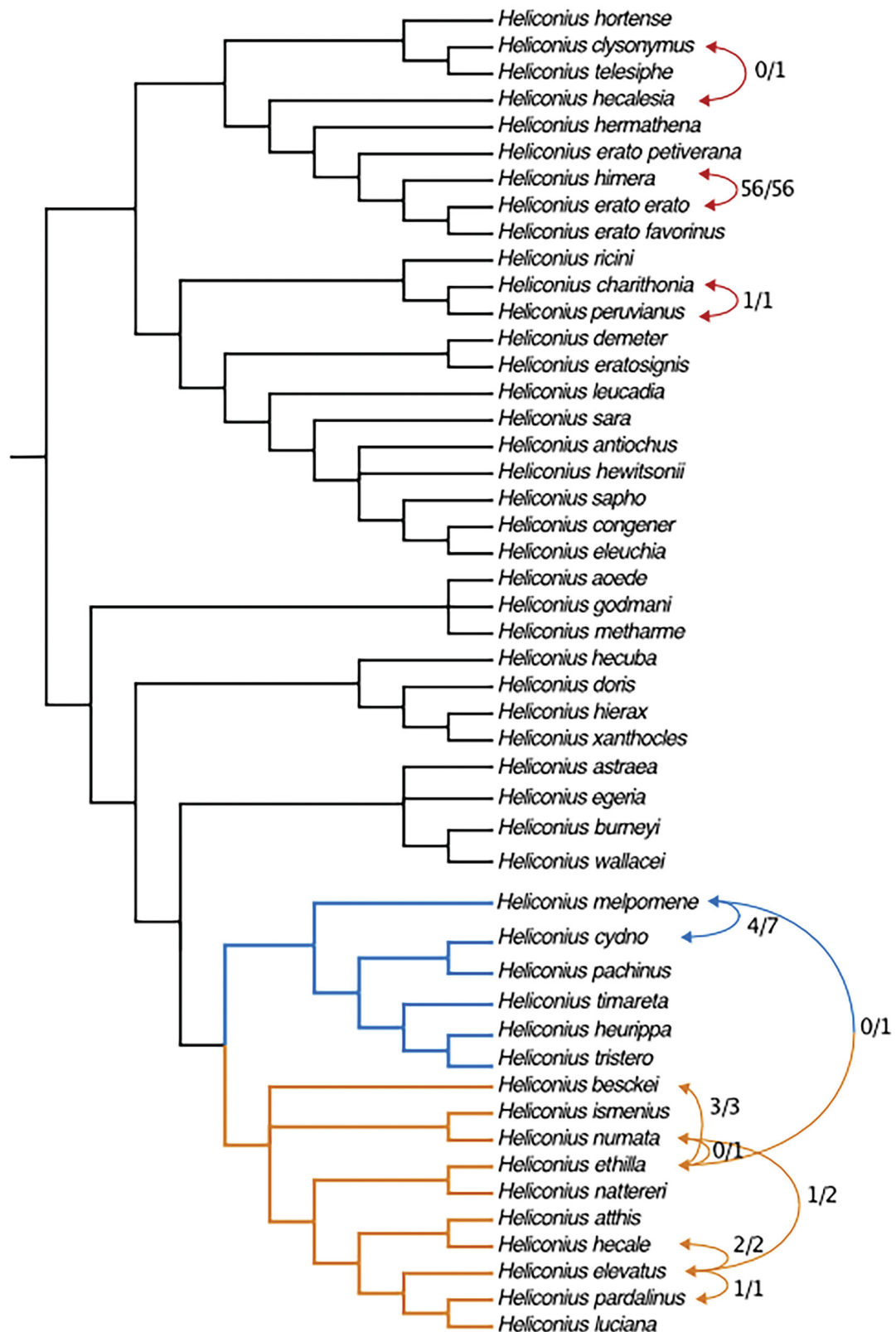


FIGURE 181. Reliable interspecific hybridization events, plotted on a parsimony consensus topology for *Heliconius* (modified from Brower & Garzón-Orduña 2018). *H. melpomene* - *H. cydno* clade indicated in blue; silvaniform clade in orange. Hybridization events are shown by the arrows. Fractional numbers indicate the number of hybrids at a 75% (numerator) or 50% (denominator) reliability cutoff (see text).

Examples of the second category (a hybrid specimen, but with incorrectly identified parents) are the several specimens hypothesized by Mallet *et al.* (2007) to be *H. melpomene*—silvaniform hybrids, but reinterpreted here as intra-silvaniform clade hybrids between *H. elevatus* and other species. Mallet *et al.* (2007) relied at several points on Keith Brown's interpretations of these specimens as *H. melpomene*—silvaniform crosses. However, Brown (1981) erroneously considered *H. elevatus* to belong to the *H. melpomene* group, rather than among the silvaniforms (despite Eltringham's (1916) demonstration that *H. elevatus* has typical silvaniform genitalia). If *H. melpomene* and *H. elevatus* were more closely related to one another than to the silvaniforms, then the degree of relatedness and time of common ancestry between either of them and any silvaniform would be the same. Given equal relatedness, Brown presumably proposed his hybrid hypotheses on the ecological grounds that *H. melpomene* is usually more common than *H. elevatus*, and therefore more likely to encounter and mate with a silvaniform species. However, since *H. elevatus* is now known conclusively to be part of the silvaniform clade (Brower, 1994a; Beltrán *et al.* 2007; Kozak *et al.* 2015; Brower & Garzón-Orduña 2018), the plausibility scales tip in favor of crosses between closer relatives within that clade. It is notable that with the alternative identifications of putative parents proposed above, the only specimen that remains a potential candidate for a *H. melpomene*—silvaniform hybrid is #06-921, captured and sequenced by Dasmahapatra *et al.* (2007), at the same time that Mallet *et al.* (2007) was in press.

For specimens falling into category three, Brower (2013) outlined a number of the challenges facing the interpretation of old, vague locality data, and also commented on the increased prevalence of commercially-traded *Heliconius* hybrids in the last few decades. It is worth repeating from that paper the statement that, "28 *H. cydno*—*H. melpomene* hybrids in the database originated with either C. Farrell, L. Denhez or J. Urbina, and wound up in the cabinets of five different amateurs." For armchair lepidopterists, collecting butterflies is akin to collecting stamps, and a bizarre hybrid *Heliconius* phenotype is like an Inverted Jenny. It is here confirmed that Chris Farrell and Leon Denhez, at least, were providers of specimens to the commercial trade. As for José Urbina, it is simply not plausible that one person (and no one else) collected eleven wild backcross *H. melpomene*—*H. cydno* hybrids at the same locality between 1980 and 2001 (almost all in fine condition, but only two ostensibly collected in the same year), and that most of these found their way into European private collections. Dismissing Brower's (2013) critique, Jiggins (2017, p. 192) said, "although it is possible that a few of the hybrid specimens may be problematic, the broad picture of hybridization in *Heliconius* is well supported." As documented above, more than "a few" of the specimens are, indeed, "problematic."

For one or more of these three reasons, the quantitative reevaluation of individual specimens presented here suggests, contrary to Jiggins' assertion, that the support for hybridization between close relatives is limited, and that support for inter-clade hybridization is vanishingly low. None of the proposed silvaniform—*H. melpomene* "hybrids," and fewer than 10% of the hypothesized *H. melpomene*—*H. cydno* hybrids, meet the 75% plausibility threshold applied here (Table 1). By that criterion, there is no evidence of hybridization events having occurred between taxa that diverged prior to the beginning of the Pleistocene (2.6 Ma). The large number of *H. himera* × *H. erato* hybrids are evidence of "interspecific" hybridization only in the semantic sense that depends upon one's preferred species concept: Mallet *et al.* (2007) employed Mallet's (1995) "genealogical cluster concept," which Brower (2000) critiqued as having no set criteria and thus being arbitrary (see further criticisms in Coyne & Orr 2004). From a phylogenetic perspective, *Heliconius himera* routinely emerges from within a paraphyletic clump of *H. erato* forms in phylogenetic trees (cf. Brower 1994b; Hines *et al.* 2011; Supple *et al.* 2015; Van Belleghem *et al.* 2017). If *H. himera* and *H. erato* are viewed as conspecific (as they traditionally were under the Biological Species Concept (Mayr, 1942) before Mallet (1993) split them asunder), then the entire database of more than 150 specimens contains only 11 plausible interspecific hybrids. Rather than supporting Mallet *et al.*'s (2007) notion of "the species boundary as a continuum," the species boundary indicated by these data seems to be a rather steep slope, if not an abrupt cliff.

Conclusion

A decade ago, when the homoploid hybrid speciation hypothesis for the origin of *H. heurippa* was proposed (Mávarez *et al.* 2006), it was critical to underpin that iconoclastic narrative with credible empirical evidence that *Heliconius* species, particularly *H. melpomene* and *H. cydno*, occasionally hybridize in nature. More recently, the notion of interspecific hybridization between *Heliconius* species has become established in conventional wisdom

through its repeated assertion as a "fact," and the empirical scaffolding can be pulled away. Mallet *et al.* (2007) seems now to be cited most often not as evidence that such hybridization occurs *per se*, but as evidence that it is rare (Mallet *et al.* 2015; Zhang *et al.* 2016; Enciso-Romero *et al.* 2017). In fact, quantified results of breeding experiments suggest that *H. melpomene* and *H. cydno* are completely reproductively isolated (Mérot *et al.* 2017, Garzón-Orduña & Brower 2018) casting doubt upon the plausibility of even the few remaining hypothetical hybrid specimens of those taxa that passed scrutiny here. Thus, hybridization among *Heliconius* species persists as a hypothetical phenomenon in a cryptobiological sweet spot, occurring too infrequently to detect in experiments, and, as shown here, supported by relatively scant evidence from collections and the field, much of which is, to say the least, subject to alternative interpretation.

Further evidence to address the frequency and importance of interspecific hybridization should be sought in three realms. First, scientists in the field should keep an eye peeled for unusual specimens that may represent hybrids. A particularly interesting area to continue searching is the vicinity of San Cristobal in western Venezuela, in order to sort out the mystery of apparent *H. melpomene* individuals with *H. cydno* genomes (Mávarez *et al.* 2006; Brower 2011). If a potential hybrid specimen is collected, it should be preserved in a manner that is amenable to genetic research, so that analysis such as that carried out by Dasmahapatra *et al.* (2007) can be performed. Data from a putative hybrid should be compared to all available sequences to ensure that the full scope of pertinent evidence is included in the assessment of the specimen's pedigree. Lastly, it is critical to conduct further lab crosses of species and geographical races that have apparently not yet been investigated (such as, for example, *H. cydno alithea* and *H. melpomene cythera*), and to preserve specimens and publish images of the resulting phenotypic diversity in F1 and F2 generations. Having such a library of the variability of known crosses will greatly facilitate the interpretation of unusual phenotypes, if and when they are discovered in the field or collections.

Heliconius is not a remarkable genus because of its species diversity. Compared to its 48 species, there are many more species-rich neotropical butterfly genera—e. g., *Dalla*, 95 spp., (Hesperiidae); *Catasticta*, 87+ spp., (Pieridae); *Euselasia*, 167 spp., (Riodinidae); and the nymphalid genera *Adelpha*, 85 spp., *Memphis*, 61 spp., *Pedaliodes*, 243 spp. (Lamas, 2004); not to mention pantropical *Actinote*, ~120 spp., Old World *Euploea* ~60 spp., *Charaxes*, ~200 spp., *Acraea*, ~130 spp.; and Holarctic *Erebia*, ~100 spp. (Wahlberg & Brower 2009). What makes *Heliconius* special is its intraspecific variation: 345 subspecies, according to Lamas & Jiggins, (2017). The phenotypic distinctness of these entities is maintained by numerically-dependent selection against phenotypically unusual hybrid offspring, despite frequent hybridization in geographical regions where they meet (Mallet and Barton, 1989). This strong selection against gene flow seems fundamentally at odds with the hypothesis of rampant interspecific introgression of wing pattern alleles that has been advanced by Jiggins (2017) and members of his research consortium. If positive numerically-dependent selection keeps freely interbreeding races of the same species from blending into one another, what even stronger evolutionary force allows wing pattern alleles to flow among distinct species which otherwise maintain their genetic integrity? As the empirical foundations of interspecific hybridization between *Heliconius* species erode, the credibility of widespread introgression diminishes, and traditional explanations for Müllerian mimicry among *Heliconius* butterflies, such as adaptive convergence, must be reconsidered.

Acknowledgments

Thanks to Ivonne Garzón-Orduña for discussion of these ideas and help with Fig. 181, and to Michel Cast for permission to reproduce the excellent photographs of *Heliconius* specimens posted on his web pages. I am also grateful to Keith Willmott and an anonymous reviewer for careful reading and thoughtful comments on the manuscript. Of course, I am solely responsible for errors and misinterpretations that may remain. This work was supported by a collaborative grant, *Dimensions US-Biota-São Paulo: Assembly and evolution of the Amazon biota and its environment: an integrated approach*, supported by the US National Science Foundation (DEB 1241056), National Aeronautics and Space Administration (NASA), and the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP Grant 2012/50260-6).

References

- Ackery, P.R. & Smiles, R.L. (1976) An illustrated list of the type-specimens of the Heliconiinae (Lepidoptera: Nymphalidae) in the British Museum (Natural History). *Bulletin of the British Museum (Natural History) Entomology*, 32, 171–214.
- Arias, C.F., Giraldo, N., McMillan, W.O., Lamas M., G., Jiggins, C.D. & Salazar, C. (2017) A new subspecies in a *Heliconius* butterfly adaptive radiation (Lepidoptera: Nymphalidae). *Zoological Journal of the Linnean Society*, 180, 805–818.
<https://doi.org/10.1093/zoolinnean/zw010>
- Arias, C.F., Salazar, C., Rosales, C., Kronforst, M.R., Linares, M., Bermingham, E. & McMillan, W.O. (2014) Phylogeography of *Heliconius cydno* and its closest relatives: disentangling their origin and diversification. *Molecular Ecology*, 23, 4137–4152.
<https://doi.org/10.1111/mec.12844>
- Aspöck, H. (1996 [1997]) Ruth Holzinger 1921–1995. *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen* 48, 65–72.
- Bates, H.W. (1862) Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society*, 23, 495–566.
- Beltrán, M., Jiggins, C.D., Brower, A.V.Z., Bermingham, E. & Mallet, J. (2007) Do pollen feeding, pupal-mating and larval gregariousness have a single origin in *Heliconius* butterflies? Inferences from multilocus DNA sequence data. *Biological Journal of the Linnean Society*, 92, 221–239.
<https://doi.org/10.1111/j.1095-8312.2007.00830.x>
- Brower, A.V.Z. (1994a) Phylogeny of *Heliconius* butterflies inferred from mitochondrial DNA sequences (Lepidoptera: Nymphalidae). *Molecular Phylogenetics and Evolution*, 3, 159–174.
<https://doi.org/10.1006/mpev.1994.1018>
- Brower, A.V.Z. (1994b) Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Sciences, USA*, 91, 6491–6495.
<https://doi.org/10.1073/pnas.91.14.6491>
- Brower, A.V.Z. (1996a) Parallel race formation and the evolution of mimicry in *Heliconius* butterflies: a phylogenetic hypothesis from mitochondrial DNA sequences. *Evolution*, 50, 195–221.
<https://doi.org/10.1111/j.1558-5646.1996.tb04486.x>
- Brower, A.V.Z. (1996b) A new mimetic species of *Heliconius* (Lepidoptera: Nymphalidae), from southeastern Colombia, as revealed by cladistic analysis of mitochondrial DNA sequences. *Zoological Journal of the Linnean Society*, 116, 317–332.
<https://doi.org/10.1111/j.1096-3642.1996.tb00126.x>
- Brower, A.V.Z. (2000) On the validity of *Heliconius tristero* and *Heliconius melpomene mocoa* Brower, with notes on species concepts in *Heliconius* Kluk (Lepidoptera: Nymphalidae). *Proceedings of the Entomological Society of Washington*, 102, 678–687.
- Brower, A.V.Z. (2011) Hybrid speciation in *Heliconius* butterflies? A review and critique of the evidence. *Genetica*, 139, 589–609.
<https://doi.org/10.1007/s10709-010-9530-4>
- Brower, A.V.Z. (2013) Introgression of wing pattern alleles and speciation via homoploid hybridization in *Heliconius* butterflies: a review of evidence from the genome. *Proceedings of the Royal Society of London B* 280, 20122302.
<https://doi.org/10.1098/rspb.2012.2302>
- Brower, A.V.Z. & Egan, M.G. (1997) Cladistics of *Heliconius* butterflies and relatives (Nymphalidae: Heliconiini): the phylogenetic position of *Eueides* based on sequences from mtDNA and a nuclear gene. *Proceedings of the Royal Society of London B*, 264, 969–977.
<https://doi.org/10.1098/rspb.1997.0134>
- Brower, A.V.Z. & Garzón-Orduña, I.J. (2018) Missing data, clade support and "reticulation": the molecular systematics of *Heliconius* and related genera (Lepidoptera: Nymphalidae) re-examined. *Cladistics*, 34, 151–166.
<https://doi.org/10.1111/cla.12198>
- Brown, K.S. Jr. (1976) An illustrated key to the silvaniform *Heliconius* (Lepidoptera: Nymphalidae) with descriptions of new subspecies. *Transactions of the American Entomological Society*, 102, 373–483.
- Brown, K.S. Jr. (1979) *Ecologia Geográfica e Evolução nas Florestas Neotropicais*. Universidade Estadual de Campinas, Campinas, xxxi + 260 + 120 pp.
- Brown, K.S. Jr. (1981) The biology of *Heliconius* and related genera. *Annual Reviews of Entomology*, 26, 427–456.
<https://doi.org/10.1146/annurev.en.26.010181.002235>
- Brown, K.S. Jr. & Fernández Yépez, F. (1985) Los Heliconii (Lepidoptera, Nymphalidae) de Venezuela. *Boletín Entomologica de Venezuela*, New Series, 3, 29–76.
- Cast, M. & Le Crom, J.-F. (2012) *Heliconius melpomene* dans le vallée de la Magdalena (Colombie): Révision et description d'une nouvelle sous-espèce polymorphique *Heliconius melpomene martiniae* nova ssp. (Lepidoptera: Nymphalidae; Heliconiinae). *Lépidoptères—Revue des Lépidoptéristes de France*, 21, 96–101.
- Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sinauer Associates, Sunderland, MA, 545 pp.
- Dasmahapatra, K.K., Silva-Vasquez, A., Chung, J.W. & Mallet, J. (2007) Genetic analysis of a wild-caught hybrid between non-sister *Heliconius* butterfly species. *Biology Letters (Royal Society)*, 3, 660–663.

<https://doi.org/10.1098/rsbl.2007.0401>

- Eltringham, H. (1916) On specific and mimetic relationships in the genus *Heliconius*, L. *Transactions of the Entomological Society of London*, 1916, 101–148.
<https://doi.org/10.1111/j.1365-2311.1916.tb03123.x>
- Enciso-Romero, J., Pardo-Díaz, C., Martin, S.H., Arias, C.F., Linares, M., McMillan, W.O., Jiggins, C.D. & Salazar, C.A. (2017) Evolution of novel mimicry rings facilitated by adaptive introgression in tropical butterflies. *Molecular Ecology*, 26, 5160–5172.
<https://doi.org/10.1111/mec.14277>
- Garzón-Orduña, I.J. & Brower, A.V.Z. (2018) Quantified reproductive isolation in *Heliconius* butterflies: implications for introgression and hybrid speciation. *Ecology and Evolution* 3, 1186–1195.
<https://doi.org/10.1002/ece3.3729>
- Gilbert, L.E. (2003) Adaptive novelty through introgression in *Heliconius* wing patterns: evidence for a shared genetic "tool box" from synthetic hybrid zones and a theory of diversification. In: Boggs, C.L., Watt, W.B. & Ehrlich, P.R. (Eds.), *Butterflies: Ecology and evolution taking flight*. University of Chicago Press, Chicago, pp. 281–318.
- Giraldo, N., Salazar, C.A., Jiggins, C.D., Bermingham, E., & Linares, M. 2008. Two sisters in the same dress: *Heliconius* cryptic species. *BMC Evolutionary Biology*, 8, 324.
<https://doi.org/10.1186/1471-2148-1188-1324>.
- Hines, H.M., Counterman, B.A., Papa, R., Albuquerque de Moura, P., Cardoso, M.Z., Linares, M., Mallet, J., Reed, R.D., Jiggins, C.D., Kronforst, M.R. & McMillan, W.O. (2011) Wing patterning gene redefines the mimetic history of *Heliconius* butterflies. *Proceedings of the National Academy of Sciences, USA*, 108, 19666–19671 and supplements.
<https://doi.org/10.1073/pnas.1110096108>
- Holzinger, H. & Holzinger, R. (1968) *Heliconius cydno gerstneri*, n. ssp. und zwei neue Formen von *H. cydno cydnides* Stgr. (Lep., Nymph.). *Zeitschrift der Arbeitsgemeinschaft Österreich Entomologen*, 20, 17–21.
- International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature*. International Trust for Zoological Nomenclature and the British Museum (Natural History), London, xxix + 306 pp.
- Jiggins, C.D. (2017) *The ecology and evolution of Heliconius butterflies*. Oxford University Press, Oxford, 277 pp.
- Jiggins, C.D., Mávarez, J., Beltrán, M., McMillan, W.O., Johnston, J.S. & Bermingham, E. (2005) A genetic linkage map of the mimetic butterfly *Heliconius melpomene*. *Genetics*, 171, 557–570.
<https://doi.org/10.1534/genetics.104.034686>
- Jiggins, C.D., McMillan, W.O., Neukirchen, W. & Mallet, J. (1996) What can hybrid zones tell us about speciation? The case of *Heliconius erato* and *H. himera* (Lepidoptera: Nymphalidae). *Biological Journal of the Linnean Society*, 59, 221–242.
<https://doi.org/10.1006/bjil.1996.0063>
- Johnson, K. & Matusik, D. (1986) A new white-and-black subspecies of *Protesilaus euryleon* (Papilionidae). *Journal of the Lepidopterists' Society*, 41, 70–74.
- Kapan, D.D. (2001) Three-butterfly system provides a field test of Müllerian mimicry. *Nature*, 409, 338–340.
<https://doi.org/10.1038/35053066>
- König, F. (1986) Ein *Heliconius erato himera*-Hybrid aus Nord-Peru (Lepidoptera, Heliconiinae). *Zeitschrift Arbeitsgemeinschaft Österreich Entomologen*, 38, 49–50.
- Kozak, K.M., Wahlberg, N., Neild, A.F.E., Dasmahapatra, K.K., Mallet, J. & Jiggins, C.D. (2015) Multilocus species trees show the recent adaptive radiation of the mimetic *Heliconius* butterflies. *Systematic Biology*, 64, 505–524.
<https://doi.org/10.1093/sysbio/syv007>
- Kronforst, M.R., Young, L.G., Gilbert, L.E. (2007) Reinforcement of mate preference among hybridizing *Heliconius* butterflies. *Journal of Evolutionary Biology*, 20, 278–285.
<https://doi.org/10.1111/j.1420-9101.2006.01198.x>
- Kronforst, M.R., Young, L.G., Blume, L.M. & Gilbert, L.E. 2006b. Multilocus analyses of admixture and introgression among hybridizing *Heliconius* butterflies. *Evolution*, 60, 1254–1268.
<https://doi.org/10.1111/j.0014-3820.2006.tb01203.x>
- Kronforst, M.R., Young, L.G., Kapan, D.D., McNeely, C., O'Neill, R.J. & Gilbert, L.E. (2006a) Linkage of butterfly mate preference and wing color preference cue at the genomic location of wingless. *Proceedings of the National Academy of Sciences, USA*, 103, 6575–6580.
<https://doi.org/10.1073/pnas.0509685103>
- Lamas, G. (1998) Comentarios taxonómicos y nomenclaturales sobre Heliconiini neotropicales con designación de lectotipos y descripción de cuatro subespecies nuevas (Lepidoptera: Nymphalidae: Heliconiinae). *Revista Peruana de Entomología*, 40, 111–125.
- Lamas, G. (Ed.) (2004) *Atlas of Neotropical Lepidoptera. Checklist: Part 4A Hesperioidea—Papilionoidea*. Scientific Publishers/Association of Tropical Lepidoptera, Gainesville, xxxvi + 439 pp.
- Lamas, G. & Jiggins, C.D. (2017) Taxonomic list. In: Jiggins, C.D. (Ed.), *The ecology and evolution of Heliconius butterflies*. Oxford University Press, Oxford, pp. 214–244.
- Linares, M. (1997) Origin of neotropical mimetic biodiversity from a three-way hybrid zone of *Heliconius cydno* butterflies. In: Ulrich, H. (Ed.), *Tropical biodiversity and systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems, Bonn, 1994*. Zoologisches Forschung Institut und Museum Alexander Koenig,

Bonn, pp. 93–108.

- Lödl, M., Keber A. & Gaal, S. (1997) Die *Heliconius*-Sammlung von Ruth und Helmuth Holzinger—nunmehr integrierter Bestandteil der Lepidoptera-Sammlung des Naturhistorischen Museums Wien (Insecta: Lepidoptera: Nymphalidae: Heliconiinae). *Entomologisches Nachrichtenblatt*, New Series, 4, 1–6.
- Mallet, J. (1993) Speciation, raciation and color pattern evolution in *Heliconius* butterflies: evidence from hybrid zones. In Harrison, R.G. (Ed.), *Hybrid Zones and the Evolutionary Process*. Oxford University Press, Oxford, pp. 226–260.
- Mallet, J. (1995) A species definition for the Modern Synthesis. *Trends in Ecology and Evolution*, 10, 294–298.
[https://doi.org/10.1016/0169-5347\(95\)90031-4](https://doi.org/10.1016/0169-5347(95)90031-4)
- Mallet, J. (2005) Hybridization as invasion of the genome. *Trends in Ecology and Evolution*, 20, 229–237.
<https://doi.org/10.1016/j.tree.2005.02.010>
- Mallet, J. (2008) Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philosophical Transactions of the Royal Society of London B*, 363, 2971–2986.
<https://doi.org/10.1098/rstb.2008.0081>
- Mallet, J. & Barton, N.H. (1989) Strong natural selection in a warning-color hybrid zone. *Evolution* 43, 421–431.
<https://doi.org/10.1111/j.1558-5646.1989.tb04237.x>
- Mallet, J., Beltrán, M., Neukirchen, W. & Linares, M. (2007) Natural hybridization in heliconiine butterflies: the species boundary as a continuum. *BMC Evolutionary Biology*, 7, 28.
<https://doi.org/10.1186/1471-2148-7-28>
- Mallet, J., Besansky, N.J. & Hahn, M.W. (2015) How reticulated are species? *BioEssays*, 38, 140–149.
<https://doi.org/10.1002/bies.201500149>
- Mallet, J., McMillan, W.O. & Jiggins, C.D. (1998) Mimicry and warning color at the boundary between races and subspecies. In: Howard, D.J. & Berlocher, S.H. (Eds.), *Endless forms*. Oxford University Press, Oxford, pp. 390–403.
- Mávarez, J., Salazar, C.A., Bermingham, E., Salcedo, C., Jiggins, C.D. & Linares, M. (2006) Speciation by hybridization in *Heliconius* butterflies. *Nature*, 441, 868–871 + 811 supplementary pages.
<https://doi.org/10.1038/nature04738>
- Mayr, E. (1942) *Systematics and the Origin of Species*. Columbia University Press, New York. 334 pp.
- de la Maza, R. (1991) *Mariposas Mexicanas*. 2nd Edition. Fondo de Cultura Económica S. A. de C. V., Mexico, D. F., 304 pp.
- Mazo-Vargas, A., Concha, C., Livraghi, L., Massardo, D., Wallbank, R.W.R., Zhang, L., Papador, J.D., Martínez-Najera, D., Jiggins, C.D., Kronforst, M.R., Breuker, C.J., Reed, R.D., Patel, N.H., McMillan, W.O. & Martin, A. (2017) Macroevo­lutionary shifts of *WntA* function potentiate butterfly wing-pattern diversity. *Proceedings of the National Academy of Sciences, USA* 114, 107021–10706.
<https://doi.org/10.1073/pnas.1708149114>
- Mérot, C., Mávarez, J., Evin, A., Dasmahapatra, K.K., Mallet, J., Lamas, G. & Joron, M. (2013) Genetic differentiation without mimicry shift in a pair of hybridizing *Heliconius* species (Lepidoptera: Nymphalidae). *Biological Journal of the Linnean Society*, 109, 830–847.
<https://doi.org/10.1111/bij.12091>
- Mérot, C., Salazar, C., Merrill, R.M., Jiggins, C.D. & Joron, M. (2017) What shapes the continuum of reproductive isolation? Lessons from *Heliconius* butterflies. *Proceedings of the Royal Society of London B*, 284, 20170335.
<https://doi.org/10.1098/rspb.2017.0335>
- Nadeau, N.J., Whibley, A.C., Jones, R.T., Davey, J.W., Dasmahapatra, K.K., Baxter, S.W., Quail, M.A., Joron, M., ffrench-Constant, R.H., Blaxter, M.L., Mallet, J. & Jiggins, C.D. (2012) Genomic islands of divergence in hybridizing butterflies identified by large-scale targeted sequencing. *Philosophical Transactions of the Royal Society of London B*, 367, 343–353.
<https://doi.org/10.1098/rstb.2011.0198>
- Naisbit, R.E., Jiggins, C.D. & Mallet, J. (2003) Mimicry: developmental genes that contribute to speciation. *Evolution and Development*, 5, 269–280.
<https://doi.org/10.1046/j.1525-142X.2003.03034.x>
- Posla-Fuentes, M. (1993) Nueva forma de *Heliconius cydno* (Lepidoptera: Heliconidae) en el Río Sarapiquí, Costa Rica. *Revista de Biología Tropical*, 41, 889–890.
- Posla-Fuentes, M. (1993) An unusual form of *Heliconius cydno* from Costa Rica (Lepidoptera: Nymphalidae: Heliconiinae). *Tropical Lepidoptera*, 4, 92.
- Poulton, E.B. (1890) *The colours of animals*. Kegan Paul, Trench, Trübner & Co., London, 360 pp.
- Punnett, R.C. (1915) *Mimicry in butterflies*. Cambridge University Press, Cambridge, 188 pp.
- Reed, R.D., Papa, R., Martin, A., Hines, H.M., Counter­man, B.A., Pardo-Díaz, C., Jiggins, C.D., Chamberlain, N.L., Kronforst, M.R., Chen, R., Halder, G., Nijhout, H.F. & McMillan, W.O. (2011) *optix* drives the repeated convergent evolution of butterfly mimicry. *Science*, 333, 1137–1141.
<https://doi.org/10.1126/science.1208227>
- Rosser, N., Phillimore, A.B., Huertas, B., Willmott, K.R. & Mallet J. (2012) Testing historical explanations for gradients in species richness in heliconiine butterflies of tropical America. *Biological Journal of the Linnean Society*, 105, 479–497.
<https://doi.org/10.1111/j.1095-8312.2011.01814.x>
- Salazar, C.A., Jiggins, C.D., Taylor, J.E., Kronforst, M.R. & Linares, M. (2008) Gene flow and genealogical history of *Heliconius heurippa*. *BMC Evolutionary Biology*, 8, 132.

<https://doi.org/10.1186/1471-2148-8-132>

- Salazar Escobar, J.A. (1993) Notes on some populations of *Heliconius heurippa* in Colombia (Lepidoptera: Nymphalidae: Heliconiinae). *Tropical Lepidoptera*, 4, 119–121.
- Schaus, W. (1913) New subspecies of Rhopalocera from Costa Rica. *Proceedings of the Zoological Society of London*, 1913, 339–367, pls. L–LIV.
- Sheppard, P.M., Turner, J.R.G., Brown, K.S. Jr., Benson, W.W. & Singer, M.C. (1985) Genetics and the evolution of Muellierian mimicry in *Heliconius* butterflies. *Philosophical Transactions of the Royal Society of London B*, 308, 433–613.
<https://doi.org/10.1098/rstb.1985.0066>
- Supple, M.A., Papa, R., Hines, H.M., McMillan, W.O. & Counterman, B.A. (2015) Divergence with gene flow across a speciation continuum in *Heliconius* butterflies. *BMC Evolutionary Biology*, 15, 204.
<https://doi.org/10.1186/s12862-015-0486-y>
- Van Belleghem, S.M., Rastas, P., Papanicolaou, A., Martin, S.H., Arias, C.F., Supple, M.A., Hanly, J.J., Mallet, J., Lewis, J. J., Hines, H.M., Ruiz, M., Salazar, C., Linares, M., Moreira, G.R.P. , Jiggins, C.D., Counterman, B.A., McMillan, W.O. & Papa, R. (2017) Complex modular architecture around a simple toolkit of wing pattern genes. *Nature Ecology and Evolution*, 1, 0052.
<https://doi.org/10.1038/s41559-016-0052>
- Wahlberg, N. & Brower, A.V.Z. (2009) Nymphalidae Rafinesque 1815. Brush-footed Butterflies. Version 15 September 2009 (under construction). The Tree of Life Web Project. Available from: <http://tolweb.org/Nymphalidae/12172/2009.09.15> (accessed 11 October 2017)
- Zhang, W., Dasmahapatra, K.K., Mallet, J., Moreira, G.R.P. & Kronforst, M.R. (2016) Genome-wide introgression among distantly-related *Heliconius* butterfly species. *Genome Biology*, 17, 25.
<https://doi.org/10.1186/s13059-016-0889-0>